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Pink Salmon Action Plan: Sea Lice on Juvenile Salmon and on Some Non-Salmonid Species in the Broughton Archipelago in 2003

Plan d'action pour le saumon rose : Pou du poisson sur les saumons juvéniles et certaines espèces de poissons autres que des salmonidés dans l'archipel Broughton en 2003

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ABSTRACT

Copepods of the family *Caligidae* (Siphonostomatoidea: Copepoda) are parasitic on the skin, fins, gills and in the buccal cavity of marine fishes. In British Columbia coastal waters these niches have been exploited by 11 species belonging to the genus *Lepeophtheirus* and two species of *Caligus*. There is little historic data on sea lice infection rates of juvenile salmonids in the Broughton Archipelago. In addition, prior to 2001, juvenile pink and chum salmon in the Broughton Archipelago had received virtually no scientific attention. Annual variations in the number and condition of out-migrating smolts from specific streams had been relatively poorly documented and their migratory routes through this region were speculative. The present study, one component of Fisheries and Oceans Canada's Pink Salmon Action Plan (PSAP), was an effort to systematically survey juvenile *Oncorhynchus* spp. for caligid copepods throughout their nearshore marine migratory phase following seawater entry. The overall objective of the study was to describe patterns of spatial and temporal variations in the prevalence and intensity (or abundance) of sea lice infections on juvenile pink and chum salmon in a limited area of coastal BC: the Broughton Archipelago and Knight Inlet. For the purpose of this study, it was hypothesized that the prevalence and intensity (or abundance) of infections on salmonid and non-salmonid fishes would be uniformly distributed temporally and spatially throughout the study.

In the present study, approximately 25% of juvenile pink and chum salmon were infected with two species of sea lice: *Lepeophtheirus salmonis* and *Caligus clemensi*. On both salmon species most infections consisted of a single sea louse and most of these were chalimus stages of *C. clemensi*. The prevalence of motile *L. salmonis* on pink salmon increased towards the end of the study, coincident with a decline in the proportion of *L. salmonis* chalimus stages. Significant variability over space and time was observed for sea lice infections on juvenile salmon, size of the juvenile salmon and seawater surface salinity and temperature. A logistic regression model developed and fit with data collected in this study demonstrated that increased probability of infection with non-motile or motile sea lice stages was related to increases in salmon fork length, seawater temperature and seawater salinity. There was no evidence that infection with sea lice adversely affected the size or condition factor of juvenile pink and chum salmon during the time that was monitored. *Caligus clemensi* and an unidentified *Lepeophtheirus* sp. were found on approximately 60% of sticklebacks. *Lepeophtheirus hospitalis* and *C. clemensi* were also found on herring.

A second component of the PSAP is reported in Hargreaves et al. (2004), the main objective of which was to regularly monitor the abundance of juvenile pink salmon at many locations during the early sea life period, to obtain additional information about the migration routes of juvenile pink salmon in the Broughton. Hargreaves et al. (2004) concluded that juvenile pink and chum salmon were widely

distributed throughout the Broughton and Knight Inlet, and that their data did not confirm or even strongly support the existence of a "main juvenile salmon migration corridor" in the Broughton.

Three recommendations derived from this work: 1, to initiate and coordinate field and laboratory studies to better understand the impact of sea lice and other infectious diseases on wild juvenile salmon; 2, to establish mechanisms for sharing relevant disease information between industry and DFO for example by initiating collaborative research programs to better understand local factors influencing prevalence, distribution and sources of sea lice infections on juvenile salmon and 3, to initiate studies to improve knowledge of the morphological characteristics of the chalimus stages of *Lepeophtheirus* species.

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RÉSUMÉ

Des copépodes de la famille *Caligidae* (Siphonostomatoidea: Copepoda) parasitent des poissons marins, se fixant à la peau, aux nageoires, aux branchies et à la muqueuse de la cavité buccale. Dans les eaux côtières de la Colombie-Britannique, ces niches ont été exploitées par onze espèces de pou du poisson du genre *Lepeophtheirus* et deux du genre *Caligus*. Il existe peu de données sur les taux d'infestation des salmonidés juvéniles par ces parasites dans l'archipel Broughton. En outre, avant 2001, presque aucune recherche scientifique n'a été faite sur les saumons roses et kétas juvéniles retrouvés dans les eaux de cet archipel. Les variations annuelles dans le nombre et la condition des smolts migrateurs issus de cours d'eau spécifiques étaient relativement mal documentées et leurs voies de migration à travers cette région avaient été établies de manière spéculative. La présente étude, un des volets du Plan d'action pour le saumon rose (PASROS) de Pêches et Océans Canada, visait à déceler systématiquement les copépodes de la famille *Caligidae* présents sur les salmonidés juvéniles du genre *Oncorhynchus* tout au long de leur migration dans les eaux littorales après leur arrivée en mer. L'objectif général de l'étude était de décrire les tendances des variations spatiales et temporelles dans la prévalence et l'intensité des infestations des juvéniles des saumons roses et kétas par les poux du poisson dans un secteur côtier limité de la C.-B. : l'archipel Broughton et l'inlet Knight. Nous avons formulé l'hypothèse à l'effet que la prévalence et l'intensité des infestations de salmonidés et de poissons autres que des salmonidés seraient uniformes au plan temporel et spatial tout au long de l'étude.

Deux espèces de pou du poisson ont été retrouvées sur environ 25 % des saumons roses et kétas juvéniles : *Lepeophtheirus salmonis* et *Caligus clemensi*. La plus grande partie des cas d'infestation se limitaient à un seul pou, la plupart étant le stade chalimus de *C. clemensi*. La prévalence du stade mobile de *L. salmonis* sur le saumon rose a augmenté vers la fin de l'étude, coïncidant à un déclin du nombre de *L. salmonis* au stade chalimus. Nous avons observé une variabilité significative dans l'espace et le temps des infestations et de la taille des saumons juvéniles, ainsi que de la salinité et de la température de la surface de la mer. Nous avons donc élaboré un modèle de régression logistique, que nous avons ajusté à l'aide des données recueillies dans le cadre de la présente étude, ce qui nous a permis de démontrer qu'il existe un lien entre la probabilité d'infestation par les stades mobiles et immobiles des poux et la longueur à la fourche des saumons, la température et la salinité de la mer : à mesure que ces variables augmentent, la probabilité d'infestation augmente aussi. Rien n'indiquait qu'une infestation avait un effet indésirable sur la taille ou le coefficient de condition des saumons roses et kétas juvéniles durant la période d'étude. *Caligus clemensi* et une espèce non identifiée de *Lepeophtheirus* ont été retrouvés sur environ 60 % des épinoches examinées, tandis que *Lepeophtheirus hospitalis* et *C. clemensi* étaient présents aussi sur le hareng.

Hargreaves *et al.* (2004) font état des résultats d'un deuxième volet du PASROS, dont l'objectif principal était de surveiller régulièrement l'abondance des saumons roses juvéniles à de nombreux endroits au début de leur arrivée en mer et d'obtenir des renseignements additionnels sur leurs voies de migration dans l'archipel Broughton. Ils ont conclu que les saumons roses et kétas juvéniles étaient distribués à grande échelle dans cet archipel, ainsi que dans l'inlet Knight, et que les données ne permettaient pas de conclure qu'il existait un corridor principal de migration des saumons juvéniles dans l'archipel Broughton, ni même d'étayer solidement cette hypothèse.

Trois recommandations découlent des résultats de cette étude : 1) lancer et coordonner des études sur le terrain et en laboratoire en vue de mieux comprendre l'impact du pou de poisson ainsi que d'autres maladies infectieuses sur les saumons juvéniles sauvages; 2) établir des mécanismes de partage des renseignements pertinents sur les maladies entre l'industrie et le MPO, par exemple, par la mise sur pied de programmes de recherche concertée visant à mieux comprendre les facteurs locaux ayant une incidence sur la prévalence, la distribution et les sources des infestations des saumons juvéniles par le pou du poisson; et 3) lancer des études en vue d'élargir la base de connaissances sur les caractéristiques morphologiques du stade chalimus des espèces du genre *Lepeophtheirus*.

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INTRODUCTION

Caligid Copepods in British Columbia

Copepods of the family Caligidae (Siphonostomatoidea: Copepoda) are parasitic on the skin, fins, gills and in the buccal cavity of marine fishes. In British Columbia (BC) coastal waters these niches have been exploited by 11 species belonging to the genus *Lepeophtheirus* and two species of *Caligus* (Table 1; see Arthur and Margolis 1979, McDonald and Margolis 1995). A diversity of specialisations is evident among these species as host specificities range from those parasitic on a single host (*L. breviventris*, *L. parvicruris*) to those parasitic on ten or more species (*C. clemensi*, *L. parviventris*, *L. salmonis*). Copepod species are distinguished from each other based on morphological criteria. In BC, caligid copepods have been reported from 44 host species representing 11 orders of elasmobranchiid, holocephaliid and actinopterygiid fish (Table 2). It is evident that these parasites, particularly those belonging to the genus *Lepeophtheirus*, have successfully adapted to the diversity of host environments available in this region. While the life histories of most of these species are not known, it is expected that these will reflect the association of each parasite and its host. In this report these parasites are collectively referred to as sea lice.

Species parasitising Pacific salmon

Three species of sea lice are reported from Pacific salmon in BC waters: *Lepeophtheirus salmonis*, *Lepeophtheirus cuneifer* and *Caligus clemensi*. Of these, *L. salmonis* is most restricted to salmonid hosts. Reports of this species on white sturgeon and sand lance are considered to represent unnatural infections (Kabata 1973). *Lepeophtheirus salmonis* has a holarctic distribution and its range overlaps with that of anadromous salmonids in the Atlantic and Pacific Oceans. The parasite is commonly found on adult Pacific salmon collected in the mid-Pacific Ocean (Nagasawa 1993, 2001) and on farmed salmon in British Columbia (Johnson and Margolis 1993). *Lepeophtheirus cuneifer* was first reported from *Raja binoculata* (big skate), *Hexagrammos lagocephalus* (rock greenling) and from as many as 8 other host species in Alaskan waters (Kabata 1974). In BC, the parasite was reported from farmed specimens of *S. salar* and *O. mykiss* (Johnson and Albright 1991a). The latter authors concluded that this species is rare on farmed salmonids in BC waters and other than its evident lack of strict host-specificity, nothing is known about its biology. *Caligus clemensi* has been reported from 13 species of salmonid and non-salmonid hosts. Knowledge of its occurrence on Pacific salmon is limited to Parker and Margolis (1964) who reported it on *O. kisutch* (coho salmon) *O. gorbuscha* (pink salmon) and *O. keta* (chum salmon). *Caligus clemensi* shows no evidence of host specificity and Parker and Margolis (1964) suggested the parasite will attach to any species of fish inhabiting surface waters. There has been no systematic surveillance of caligid copepods on juvenile

or adult salmon in BC coastal waters. Therefore, temporal and geographic variations in the prevalence and intensity of infections on Pacific salmon along coastal BC waters are not known.

Life cycle of caligid copepods

The developmental biology of sea lice varies little among genera and species and has been reviewed elsewhere (Costello 1993, Johnson 1998, Pike and Wadsworth 1999). Of the species occurring in BC, developmental stages are well described for only *C. clemensi* and *L. salmonis* (Fig. 1). Generally, following egg hatch two sequential stages of free-swimming nauplii give rise to a free-swimming copepodid. The copepodid seeks out and attaches to the host. Once attached, the parasite develops by molting through four chalimus stages that are firmly attached to the host by a frontal filament and are therefore considered non-motile. The fourth chalimus is followed by pre-adult and adult stages that are referred to as motile. Adults mate while on the fish and the fertilised female produces egg strings. Water temperature and salinity regulate the rate of copepod development and of nauplii and copepodid survival. Development is accelerated with increased water temperature and survival is enhanced with increased salinity. Dispersal of planktonic stages depends on tidal flows and when near a potential host, copepodids rely on chemical, optical and mechanical cues for host location (Heuch and Karlsen 1997, Ingvarsdóttir et al. 2002). Planktonic stages do not feed and their longevity depends on the availability of stored energy. Adults and pre-adults of *Caligus* spp. may also be found among the seston as movement of these stages among hosts is not uncommon (Pike and Wadsworth 1999).

Pathological consequences of infection

Sea lice feed on mucus, skin and blood. The area affected by feeding activities of smaller, attached stages (for example the chalimus) is limited to the point of attachment. In contrast larger, the larger motile stages have greater potential to cause more extensive damage and in practise, disease is associated with the feeding activities of these stages. The ability of pathogens (viruses, bacteria, parasites) to cause disease in fish is intimately linked to factors associated with the host as well as to the number and virulence of the pathogen (Stephen 1991). Environmental factors also contribute to the impact of a pathogen and must be considered to understand pathogen impact. Factors contributing to pathology and disease caused by sea lice include species, age (size) and condition of fish as well as the number, stages and species of lice involved. Susceptibility to laboratory infections varies among species with Atlantic salmon being more susceptible, chinook intermediate and coho salmon most resistant (Johnson and Albright 1992, Fast et al. 2002). Morbidity due to severe infections with *L. salmonis* preferentially occurs among smaller size classes of Atlantic salmon and sea trout smolts and is typically associated with pre-adult and adult lice stages

(Bjørn and Finstad 1997, Grimnes and Jakobsen 1996). Infections with *motile* stages of *L. salmonis* infections that are sufficiently severe elicit a stress response, reduced macrophage activity and altered haematological parameters in laboratory infected salmonids (Mustafa et al 2001, Wagner et al. 2003, Wagner and McKinley 2004). More recent work however, also implicates non-motile stages in eliciting immunodepression in the host (Fast et al. 2002). These observations suggest that sea lice infections directly or indirectly increase host susceptibility to other infections. Nothing is known about the innate susceptibility of other species of Pacific salmon to *L. salmonis* infestations and of the intensity of motile or non-motile stages required to cause disease.

The present study

Much of the effort to understand the epizootiology of sea lice infections on salmon has focused on host species occurring in the Atlantic Ocean (e.g., *Salmo salar*, *Salmo trutta*) and particularly on larger farmed salmon with several months or more of exposure to the marine environment (Revie et al., 2002b; Revie et al., 2003). Prior to 2001, juvenile pink and chum salmon in the Broughton Archipelago had received virtually no scientific attention. Annual variations in the number and condition of out-migrating smolts from specific streams were poorly documented and their migratory routes through the Archipelago were speculative. There is virtually no information on the epizootiology of sea lice on juvenile Pacific salmon (*Oncorhynchus* spp.) following their migration into the nearshore environment. These knowledge gaps challenged the interpretation of claims made in 2001 and 2002 that juvenile pink and chum salmon in the Broughton Archipelago were infested with unusually high levels of sea lice (Morton et al. 2004). This uncertainty led to considerable speculation regarding the origin and impact of sea lice infestations on juvenile Pacific salmon (Anonymous 2002), and to the possibility of a relationship between sea lice infestations on juvenile salmon and the abundance of these salmon that survive to spawn (Anonymous 2002).

Morton et al. (2004) concluded that the distribution and abundance of *L. salmonis* and *C. clemensi* on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in part of the Broughton Archipelago region of British Columbia, Canada was related to the proximity of active salmon farms. The oceanographic characteristics of this region are influenced by heavy precipitation in winter and spring and by snowmelt in mid to late summer. In addition, the combined effects of freshwater inflow, winds and tidal action result in a net seaward flow of surface (0m to ~35m) water through the region by 8 to 15 cm/sec (Dario Stucchi, Fisheries and Oceans Canada, personal communication). Following entry into this marine habitat, juvenile salmon will therefore encounter salinity and thermal gradients as they migrate towards the open ocean. In addition, during this nearshore migration daily increases in body mass among juvenile pink and chum salmon range from three to seven percent (Heard, 1991; Salo, 1991). Given the

evident complexity in this region of oceanographic and biological characteristics known to influence sea lice, these factors should be carefully documented in efforts to understand the epizootiology of these parasites.

The present study is an effort to systematically survey juvenile *Oncorhynchus* spp. for caligid copepods throughout their nearshore marine migratory phase following seawater entry. The study was not designed to answer questions relating to the origins of parasitic copepods on wild juvenile salmon. Rather, the data were expected to provide a reference database to assist in the formulation of more focused hypotheses in future efforts.

In this study, infections of fish with parasitic copepods are described using the terminology of Margolis et al. (1982). Prevalence is the percent of infected fish in a sample, intensity is the mean number of lice on infected fish in a sample, and abundance is the mean number of lice per fish for all fish in a sample. The overall objective of the study was to describe patterns of spatial and temporal variations in the prevalence and intensity (or abundance) of sea lice infections on juvenile pink and chum salmon in a limited area of coastal BC: the Broughton Archipelago and Knight Inlet. For the purpose of this paper, it is hypothesized that the prevalence and intensity (or abundance) of infections on salmonid and non-salmonid fishes would be uniformly distributed both temporally and spatially.

METHODS

A detailed description of sampling dates, sites and gear used are provided in the accompanying PSARC paper (Hargreaves et al. 2004). Briefly, fish were collected from over 115 sites each week for 15 weeks. The study area was initially divided into 11 zones to facilitate the analysis of geographic variation. The boundaries of zones A to E were chosen to subdivide the entire length of Knight Inlet into approximately equal lengths. The six remaining zones were based on naturally occurring divisions among larger reaches and channels within the Broughton area (Fig. 2). Figure 3 illustrates the location of the salmon farm sites that were fallowed within the Broughton Archipelago during the present study that occurred between March 3, 2003 and June 13, 2003. An effort was made at each site to collect fish using both purse and beach seines. See Hargreaves et al. (2004) for details relating to method of sub-sampling fish from the gear. The direct bagging method was felt to minimise the risk of losing lice, however counts of motile *C. clemensi* (and probably copepodid stages) were probably underestimated due to the spontaneous swimming behaviour displayed by this species. Following their collection and bagging, frozen fish were shipped to the Pacific Biological Station (PBS) for further analysis. Emphasis was placed on the examination of juvenile pink and chum salmon. Three-spine sticklebacks were also examined because a high prevalence of lice on this species was observed in early samples. On a set-by-set basis, fish were thawed and fork length and wet weight were determined. The

identity of the fishes were confirmed using standard taxonomic keys and when necessary, by consulting the appropriate experts at the PBS. Each fish was examined for parasitic copepods and for evidence of damage to skin or fins using a stereoscopic, dissecting microscope. These fish data as well as the number and location of copepods were entered onto a standardized laboratory data sheet. Motile stages were immediately identified to species. All infected fish were stored in 10% neutral buffered formalin, pooled by set and species, for subsequent identification of non-motile (chalimus) stages. The criteria used to identify lice to species and stages were taken from Johnson and Albright (1991), Kabata (1972) and Kabata (1973) and are described in Appendix 1. Of the 11 species of *Lepeophtheirus* reported from fish in British Columbia, the chalimus stages of only *L. salmonis* have been described. Similarly, only the chalimus stages of *C. clemensi* are well described. Therefore, while it is likely that the *Lepeophtheirus* chalimus reported here from juvenile salmon belong to *L. salmonis*, they are identified only as *Lepeophtheirus* spp. Most lice were identified at the PBS, however samples were also provided to other laboratories for identification. Sea lice data are divided into three infection categories for prevalence and abundance analysis: motile *L. salmonis*, motile *C. clemensi* and total immature stages (includes copepodid and chalimus stages of *L. salmonis* and *C. clemensi*). Identified chalimus stages are expressed as relative proportions sampled from the infected population.

Surface seawater temperature and salinity data were collected using methods described in the accompanying paper (Hargreaves et al. 2004). Temperature data were obtained from all zones except zone A between weeks 5 and 15. Sporadic sampling for temperature was conducted earlier. Similarly, salinity samples were obtained in week 6 and between weeks 9 and 15. Not all zones were sampled for salinity in weeks 6 and 14.

Catch, fish and lice data were compiled in a Microsoft Access database. Database version 4.6 was used to conduct quantitative analyses. Data summaries and trends were depicted both by zone and week. To increase the effective sample sizes in those zones where the abundance of sea lice was low, zones were combined into four consolidated areas (ABCJ, DF, EHK and GI) based on the approximate distance of zones from the open ocean. The consolidated areas were used for further analyses. Salmon outliers were identified by fitting mass-length regression models and those fish with standardized residuals that exceeded 5.5 on first or second iteration were checked for errors and in cases where appropriate corrections could not be applied, were omitted from subsequent analyses. Two-way (week, area) analysis of variance (ANOVA), using log-transformed data, was used to test the significance of spatial and temporal variations in fork length and wet mass for each species. A similar analysis tested the significance of variations in non-transformed temperature data (weeks 5 to 15). In addition, pair-wise comparisons of length, mass and temperature data from each area were made

using the Tukey method. Two-way (week, area) analysis of variance was used to test the significance of temporal and spatial variations within the salinity data (weeks nine to 15). Similarly temporal and spatial variations within the prevalence data were tested using generalized linear models (with binomial family and logit link functions) for all infection categories on each of chum and pink salmon. To compensate for low positive set counts (i.e., those containing infected fish) in individual weeks, temporal data for the latter models were divided into two categories: early (weeks 1 to 7) and late (weeks 8 to 15). Within each area and time category block, infections were coded on a set-by-set basis (1 = lice present, 0 = lice absent) and all sets containing the species of salmon in question were included. Statistical significance throughout this study was based on P=0.05.

First approximations of the relationship between the occurrence of sea lice on salmon, oceanographic data and fish characteristics were derived by fitting a logistic regression model using the SAS macro GLIMMIX. The model estimated the probability (p) of one or more sea lice being found on a fish. Geographic area, fish length and mass, temperature and salinity were considered as possible predictors for weeks 6 to 15, the period during which temperature and salinity, as well as length and mass were measured. The functional form of the fitted model is

$$p = e^{?}/(1+e^{?}),$$

where

$$? = b_0 + b_{DF}Area_{DF} + b_{GI}\,Area_{GI} + b_{EHK}\,Area_{EHK} + b_{mass}Mass + b_{length}\,Length + b_{temperature}Temperature + b_{salinity}Salinity + e_{catch}.$$

In this model, b_0 is an intercept related to the prevalence among fish caught in Area ABCJ, whereas b_{DF}, b_{GI} and b_{EHK} are respectively parameters (log odds) that measure the relative change (i.e., compared with the prevalence in Area ABCJ) in prevalence among fish caught in Areas DF, GI and EHK; $Area_{DF}$, $Area_{GI}$ and $Area_{EHK}$ are the corresponding indicator (0,1) variables denoting location in Areas DF, GI, EHK (e.g., Area DF = 1 if Zone = D or F and 0 otherwise). Similarly, b_{length}, b_{mass}, $b_{temperature}$ and $b_{salinity}$ are parameters (log odds) that measure the effect of changes in fork length, wet mass, water temperature and salinity, respectively; the variables Mass, Length, Temperature and Salinity are self-explanatory. Finally e_{catch} is a random effect (assumed to be normally distributed with mean 0 and variance s^2) representing the random variation among catches. Prevalence models for each of motile *C. clemensi*, motile *L. salmonis* and total immature stages were fit separately for pink and chum salmon. A sub-sample of 67% of the data was used to derive the models and the remaining 33% of the data were used to construct receiver operating characteristic (ROC) curves for model validation (Hanley, 1989). The ROC curve is a graphical demonstration of the predictive power of a (binary) logistic model that plots sensitivity (i.e., probability that an infected fish is correctly predicted to be infected) versus 1-specificity (i.e., probability that an uninfected fish is erroneously predicted to be infected), where in this case, a fish is predicted to be infected whenever $p \geq T$ and T is allowed to vary between 0 and 1.

Two-way ANOVA (infection x week) analyses using log-transformed length and weight data were used to provide weekly estimates of the effects of lice (motile *Lepeophtheirus*, motile *Caligus*, total immature stages) on apparent growth rate and Fulton's condition factor ($k=100 \times (\text{body weight}) / (\text{fork length})^3$).

RESULTS

Numbers of samples

A total of 11,271 chum salmon, 7,438 pink salmon and 2,815 three-spine sticklebacks were examined in the laboratory. The mean weekly sample sizes of chum and pink salmon and sticklebacks were 751, 496 and 188, respectively (Tables 3 to 5). Pink salmon and sticklebacks were collected from all zones except zone A and chum salmon were collected from all zones. The mean sample sizes of chum and pink salmon and sticklebacks among zones were 1025, 744 and 282, respectively (Tables 3 to 5).

Sizes of fish

During the course of the study mean wet mass of chum and pink salmon increased from 0.4g to 6.1g and from 0.2g to 5.5g, respectively (Fig. 4). Similarly, the corresponding mean fork lengths increased (Fig. 5). Mean length and mass of pink and chum salmon differed among zones (Figs. 6, 7). Statistically, fork length and wet mass of both salmon species varied significantly among consolidated areas and weeks and interactions between these effects were also significant (Figs. 8, 9). Among chum and pink salmon, was compared with areas EHK and GI and when area EHK was compared with GI (Tables 6, 8). The significance of differences of fish masses compared between areas was similar to those of length except the mean masses of chum salmon from areas EHK and GI were not significantly different (Tables 7, 9).

Sticklebacks remained similar in length (~63mm) and weight (~3.4g) between weeks 6 and 15 (Figs. 4 to 7). Lengths and weights of sticklebacks, while variable, tended to be similar among areas.

Infections with sea lice

Overall, sea lice were found on 27.1% of chum salmon, on 24.0% of pink salmon and on 61.3% of 3-spine sticklebacks (Table 10). The intensities of sea lice infections were 2.18 on chum salmon, 1.65 on pink salmon and 5.95 on sticklebacks. Although mean intensities were low, a small number of individual salmon and sticklebacks were found to have much higher numbers of sea lice as indicated by the ranges (Table 10).

Non-motile (immature) stages

Salmon: Copepodids and chalimus stages were observed on 23.5% of chum and 17.2% of pink salmon (Table 11). Most infections consisted of chalimus stages and the prevalence of all immature stages by varied by week and zone. On pink and chum salmon the prevalence was greatest in zones H followed by K, G and F and least in zones C, I and J (Fig. 10). Similar patterns of significant variation were evident in the prevalence of non-motile stages on pink and chum salmon among consolidated areas and over time (Figs. 11, 12; Table 12). Chalimus and copepodids were over-dispersed within the juvenile pink and chum populations as 2 or more stages were found on only 5.8% of pink and 11.3% of chum. In contrast, 2 or more chalimus or copepodids were found on 49.8% of the stickleback population (Fig. 13).

A total of 4,284 (58%) of copepodid and chalimus stages were identified to stage and genus. Of the 1,184 identified from pink salmon, 60.1% were *Caligus* and 39.9% were *Lepeophtheirus*. Similarly, of the 3,100 identified from chum salmon, 64.8% were *Caligus* and 35.2% were *Lepeophtheirus*. A uniform distribution of *Lepeophtheirus* life history stages (copepodid to chalimus 4) was observed on both salmon species (Fig. 14). In contrast, *Caligus* stages on both salmon species were predominantly chalimus 1 with declining proportions of chalimus 2, 3 and 4. The *Caligus* copepodid was observed considerably less frequently than the *Lepeophtheirus* copepodid (Fig. 14). Combined copepodid and chalimus data are presented as relative proportions of *Caligus* and *Lepeophtheirus* by week and zone (Figs. 15 and 16). The relative proportion of *Caligus* to *Lepeophtheirus* immature stages increased on both pink and chum salmon in the latter half of the study. There was no consistent pattern in the relative proportions of *Lepeophtheirus* and *Caligus* immature stages among zones on either pink or and chum salmon.

Sticklebacks: Copepodids and chalimus stages were observed on 60.7% of 3-spined sticklebacks. Of the 2,872 of these specimens that were identified to stage and to genus, 93.6% were *Caligus* and 6.4% were *Lepeophtheirus*. The distribution of *Caligus* immature stages ranged from 19% (chalimus 2) to 29.5% (chalimus 1) (Fig. 14). As on salmon, the *Caligus* copepodid was infrequently observed on stickleback.

***Motile* Lepeophtheirus salmonis**

Salmon: Motile stages of *L. salmonis* were found on 4.4% of chum salmon and 6.0% of pink salmon (Table 11). Initially the weekly prevalence on pink and chum salmon was similar, increasing from less than 2% before week 9 to approximately 12% in week 12. During weeks 13 to 15 the prevalence on chum

remained between 6.4% and 7.1% whereas on pink, the prevalence increased to 15.8% (Fig. 17). The prevalence of motile *L. salmonis* over all weeks on juvenile pink and chum salmon showed considerable spatial heterogeneity being greatest in zones K (8.1%, 9.2%), H (13.2%, 9.0%) and F (11.8%, 8.3%) and least in zones B (0.9%, 0.9%), C (1.7%, 1.7%), I (0.9%, 1.2%) and J (0.4%, 1.2%) (Fig. 18). Similar patterns of significant variation were evident in the prevalence of motile stages of *L. salmonis* on pink and chum salmon among consolidated areas and time (Figs. 19, 20; Table 13). Motile *L. salmonis* occurred with increasing frequency in the latter half of the study on both salmon species.

Approximately 1.1% of chum and 1.2% of pink salmon were infected with 2 or more motile *L. salmonis* (Fig. 21). The abundance of motile *L. salmonis* on pink and chum salmon remained low (<0.05, not shown) from weeks 1 to 8, increased to week 12, remained constant or declined to week 14 then on pink salmon, increased sharply in week 15. The abundance of motile *L. salmonis* on pink and chum salmon was greatest in zones F and H and least in zones B and I. Most infections consisted of a single motile parasite therefore the prevalence and abundance curves were similar.

Sticklebacks: A motile *Lepeophtheirus* sp. was observed sporadically throughout the study. This parasite was not *L. salmonis* and its identity was not determined. The prevalence peaked to 15% in week 3 then again to 12% in week 12. The prevalence was highest (9%-12%) in zones F, G and H. and least (<1%) in zones C, I and J.

***Motile* Caligus clemensi**

Salmon: Motile stages of *C. clemensi* were found on 3.5% of chum salmon and 4.0% of pink salmon (Table 11). The prevalence on pink and chum salmon increased over the course of the study from less than 1% in week 2 to approximately 6% in week 14. The prevalence on both species increased in week 15 to approximately 25% (Fig. 22). The prevalence varied among geographic zones and was greatest on pinks in zone F (10.7%) and on chum in zone H (9.9%). The prevalence was least in zone I both on pink (0.15%) and chum (0.19%) salmon (Fig. 23). Similar patterns of significant variation were evident in the prevalence of motile stages of *C. clemensi* on pink and chum salmon among consolidated areas and over time (Figs. 24, 25; Table 14). As with motile *L. salmonis*, motile *C. clemensi* occurred with increasing frequency on pink and chum salmon in the latter half of the study.

Approximately 1% of pink and chum salmon were infected with two or more motile *C. clemensi* (Fig. 26). The weekly abundance of motile *C. clemensi* was very similar on pink and chum salmon (not shown). Abundance on both species gradually increased to approximately 0.10 lice per fish by week 14 then markedly

increased to approximately 0.40 lice per fish. The abundance (not shown) on pink salmon was greatest in zones F and H (0.13 lice per fish) and on chum salmon in zone H (0.19 lice per fish). The abundance on both species was least in zone I (0.001 and 0.002 lice per fish, respectively).

Sticklebacks: Motile *C. clemensi* increased in prevalence from zero in week 1 to peaks of 23.5%, 24.7% and 30.9% in weeks 4, 9 and 12, respectively (Fig. 22). Motile *C. clemensi* was most prevalent in zones F (27.9%), H (19.1%) and D (16.6%) and least prevalent in zone J (0.6%) (Fig. 23). The abundance (not shown) peaked at 0.5 lice per fish in week 12. Similarly, abundance was greatest (0.43 lice per fish) in zone F and least (0.006 lice per fish) in zone J.

Seawater temperature and salinity

Mean surface seawater temperature ranged from 7.0°C to 16.3°C between weeks five and 15 and among the study areas (Fig. 27). Trends of increasing temperature were evident in all areas (Fig. 27). Significant differences in temperature were found over weeks and between all area pairings except DF and EHK (Table 15). Statistical interactions between areas and weeks were significant. The mean surface seawater salinity ranged from 3.6 parts per thousand (ppt) to 28.6 ppt during the study. Mean salinity declined from 21.9 parts per thousand (ppt) in week 6 to 15.5 ppt in week 15 (Fig. 28). Compared with area ABCJ, salinity was significantly higher in areas DF and EHK but not in GI. Similarly, salinity was significantly lower during weeks 13 to 15 compared with week 9 (Fig. 28; Table 16).

Modeling the risk of sea lice infection

Significant spatial and temporal variability was observed in the size of the juvenile salmon, seawater salinity, temperature and in the prevalence of infections with motile *Lepeophtheirus*, motile Caligus and non-motile lice stages of both species. A logistic regression model was developed from these data to predict the prevalence (probability a fish is infected with 1 or more lice) of infections on pink and chum salmon. The coefficients (log odds) calculated for the parameters used in models fit for chum and pink salmon infected with motile *C. clemensi* or *L. salmonis* or with total immature lice stages are given in Table 17. Probabilities of infection in consolidated area EHK were estimated for each of pink and chum salmon from fitted models for selected values of length, salinity and temperature representative of those found in the dataset (Fig. 29, 30).

The probability of infection with immature stages (copepodids and chalimi of both species) increased with salinity and fish length: to 75mm in chum and to 50mm in pink salmon. Predicted prevalences were lower on larger fish. No effect of temperature was evident in chum or pink salmon. The probability varied among zones and was greatest for both species in EHK (Table 17).

The probability of infection of chum with motile *L. salmonis* increased with temperature, salinity and fish length to 100mm, but decreased between 100mm and 125mm. On pink salmon, similar patterns were estimated although an effect of temperature was not evident. On both species, the probability of infection varied among areas and was greatest on chum in area EHK and on pink in area GI.

The probability of infection with motile *C. clemensi* increased with temperature, salinity and fish length for both salmon species and was greatest for chum of 100mm and for pink of 125 mm. On chum, the probability of infection varied among areas and was greatest in DF whereas on pink no effect of area was evident. The relative predictive power of the Model as determined from receiver operating characteristic curves was greatest both for motile *C. clemensi* and total immature stages on chum salmon and for motile *C. clemensi* on pink salmon (Fig. 31).

Estimating the impact of infection

Log-transformed wet mass and fork length were compared at weekly intervals for uninfected pink and chum salmon and those infected with motile *Lepeophtheirus*, motile *Caligus* and with non-motile stages of both lice species. Significant increases in the wet mass of both pink and chum occurred between weeks 1 and 15, whether salmon were infected with caligid copepods or not. There was no significant difference of either length or weight between uninfected pink salmon and those infected with non-motile stages (Fig. 32; Table 18). Where respective differences in length and mass of uninfected pink and chum salmon and those infected with motile stages of *Lepeophtheirus* and *Caligus* were significant, infected fish tended to be larger (Figs. 33, 34; Tables 19, 20). Condition factors of pink and chum salmon were not different or were significantly higher in infected salmon compared with uninfected salmon (Figs. 35 to 37, Tables 18 to 20).

DISCUSSION

This study provides the first evidence of sea lice infections among juvenile *Oncorhynchus* spp. immediately following entry into the marine nearshore environment throughout the Broughton Archipelago and Knight Inlet area of British Columbia. These observations and conclusions will assist in our understanding the factors that regulate sea lice infections on juvenile salmon and co-occurring species in this region. Approximately 25% of juvenile pink and chum salmon and 59% of stickleback were infected with sea lice in the spring of 2003. Two species of sea lice were observed on the salmon (*Caligus clemensi* and *Lepeophtheirus salmonis*) and two species on the stickleback (*C. clemensi* and an unidentified *Lepeophtheirus* sp.). Non-motile sea lice (chalimus and copepodids) were the most frequently observed stages (17.2% of pink, 23.4% of chum, 58.5% of stickleback)

and most of these (63.5% on salmon, 93.6% on stickleback) were *C. clemensi*. Motile (preadult and adult) stages of both species were also observed, albeit less frequently. The analyses of prevalence and abundance support a conclusion of significant spatial and temporal variation in the occurrence of motile (preadult and adult) and non-motile stages of *Lepeophtheirus salmonis* and *Caligus clemensi* on juvenile pink and chum salmon throughout the study area. Similarly, significant spatial and temporal variation in salinity, temperature and size of the juvenile salmon was documented. The occurrence of sea lice on stickleback, a year-round resident within this marine area, provides further insight into the complex life history of *C. clemensi*. In general however, very little is known about the factors regulating the epizootiology of *L. salmonis* or *C. clemensi* whether on wild or farmed fish (Revie et al. 2002). The association of various environmental and biological variables with the observed patterns of sea lice distribution is discussed. A comparison of the condition factor, length and mass of infected and uninfected salmon as indicators of the possible impact of sea lice infection is also discussed.

The onset of sampling in this study coincided closely with the observed out-migrations of juvenile pink and chum salmon from streams draining into the study area (Gordon McEachen, Fisheries and Oceans Canada, personal communication). In addition, mean fork lengths of salmon sampled in the first five weeks of the study coincided closely with the size of recent marine migrating juveniles throughout the range of these species (Heard, 1991; Salo, 1991). The sampled juvenile salmon were assumed to have migrated from streams located within the Broughton - Knight Inlet area and size was therefore considered a useful estimator of relative marine residence time. Stocks of origin were not determined however, and it is possible that some fish caught in particularly more exposed locations (e.g., zone E) may have derived from more southerly drainage basins (e.g., the Fraser River). In any event, the small pink and chum salmon from some areas (e.g. ABCJ) suggested a greater proportion of more recent marine migrants. Low prevalences of both lice species were consistently observed on salmon in area ABCJ and trends of increasing prevalence with increased size of both salmon species were supported by logistic regression modelling. The probability of infection with immature lice stages was greater in smaller salmon at cooler temperatures and larger more heavily infected salmon were collected later in the year from waters that were relatively warm. These results suggest that increased host size was associated both with greater prevalences of infection and with infections comprising more-advanced sea lice developmental stages. The tendency of the predicted prevalence of motile *L. salmonis* on pink and chum and *C. clemensi* on chum to decline on the largest hosts may reflect losses due to aging or detachment of lice or to the development of host immunity. Together, these observations support previous work on captive and wild salmonid populations in which prevalence and intensity of infections were related both to duration of exposure to the planktonic infective stage (Tully 1989, Tully and Whelan 1993, Nagasawa et al. 1993, Nagasawa et al. 2001),

and to the effects of temperature on sea lice egg hatch success and subsequent developmental rates (Johnson and Albright 1991).

Significant spatial and temporal variation in surface salinity was recorded during this study. Consistent with the predicted adverse influence of reduced salinity on sea lice infections, the prevalence of motile *L. salmonis*, motile *C. clemensi* and all non-motile stages were lowest on pink and chum salmon in areas with low salinity. Furthermore, logistic regression models consistently predicted that higher probabilities of infection with all lice stages on both salmon species were associated with higher salinity. Similarly in coastal Norwegian waters, levels of infection with *L. salmonis* on sea trout (*Salmo truttae*) that overwinter are influenced by temperature and salinity which vary from year-to-year (Heuch et al., 2002). In general, caligid copepods have limited capacity to survive or develop in brackish or more diluted seawater (see Pike & Wadsworth, 1999). While adult *L. salmonis* may survive a few days in freshwater (Wootten et al., 1982; Hahnenkamp & Fyhn, 1985), early developmental stages are most susceptible to the deleterious effects of reduced salinity (Berger, 1970; Johnson & Albright, 1991). Eggs hatch but the nauplii do not survive in water with salinity of only 15 parts per thousand (ppt) (Johnson & Albright, 1991). Tucker et al. (2000) reported more rapid growth and settlement of juvenile *L. salmonis* at 34 ppt compared with 24 ppt seawater. Although salinity significantly influences survival and development of *L. salmonis*, surprisingly little is known about its role in the epizootiology of *Caligus* spp. (Revie et al., 2002a). The present observations however, demonstrated reduced salinity was also associated with a lower prevalence of *C. clemensi* on both salmon species and on sticklebacks suggesting an adverse impact on this parasite species. Interestingly, laboratory studies showed that *L. salmonis* copepodids were not always associated with the highest salinities when exposed to experimental gradients (Heuch 1995). In the latter study, copepodid behaviour in response to salinity and light was thought to be adaptive, maximising the probability of host detection. The tendency of juvenile pink and chum salmon to occupy surface or near-surface waters observed in the present study supported previous observations (Heard, 1991; Salo, 1991, Morton et al., 2004) and confirmed the relevance of associating surface temperatures and salinities with sea lice data. Given the capacity for vertical migration displayed by planktonic caligid larvae (Heuch et al. 1995) however, future studies may benefit by also collecting temperature and salinity data from deeper within the water column.

A noteworthy observation was the overall similarity in prevalence and abundance of motile *L. salmonis*, *C. clemensi* and of all non-motile stages on juvenile pink and chum salmon. This similarity was apparent both in spatial and temporal summaries of the data and suggested that these species, perhaps because of similarities in habitat usage, were exposed to similar levels of infection. In addition, it is possible that both salmon species share similar physiological susceptibilities to the sea lice species. In contrast, the prevalence and intensity of

C. clemensi on sticklebacks throughout the study was considerably higher than on the salmon species. It is not clear whether sticklebacks are more susceptible to *C. clemensi* or whether their behaviour or distribution in the water column brings them more frequently into contact with copepodids. Infections on both salmon species were predominantly chalimus stages and most of the chalimus belonged to *Caligus clemensi*. During the course of the study the relative proportion of *Caligus* to *Lepeophtheirus* chalimus stages increased on both pink and chum salmon, suggesting continual exposure to *C. clemensi* copepodids and/or a maturation of *L. salmonis* to motile stages. When comparing chalimus on pink and chum, there was no consistent pattern in the relative proportions of *Lepeophtheirus* and *Caligus* among zones. In addition, the distribution of copepodid and chalimus stages was distinct for both *Lepeophtheirus* and *Caligus* and this distinction was evident on both salmon species. Similar proportions of copepodid and chalimus stages typified *Lepeophtheirus*, whereas for *Caligus* the chalimus 1 and 2 stages were most abundant (~80%). This difference supports the "continual exposure to Caligus" hypothesis. Alternatively, a relatively higher rate of loss among later *Caligus* chalimus stages may have occurred on the salmon. Both mechanisms may have occurred simultaneously. It was interesting to note that on stickleback, the relative proportions of *Caligus* chalimus stages 1 to 4 were similar to each other, reminiscent of the proportions of *Lepeophtheirus* chalimus on salmon. Given that sticklebacks evidently shared the same habitat as the juvenile salmon during the study period, it is assumed that sticklebacks were exposed to similar levels of infection with *Caligus* copepodids as were experienced by the juvenile salmon. Despite this, sticklebacks were consistently infected with higher proportions of late *Caligus* chalimus and the prevalence and abundance of motile *Caligus* were double those on juvenile salmon. Together with the relatively lower prevalence and abundance, the low proportion of late *Caligus* chalimus stages suggests that juvenile salmon are less suitable hosts to this parasite and infections were limited through unknown mechanisms. Juvenile salmon may therefore play a relatively small role as temporary hosts of *C. clemensi* in the nearshore environment. In contrast, three-spine stickleback, because of their abundance and persistence in the area, combined with the abundance of *C. clemensi* on this host, appeared to play more important role in the epizootiology of this parasite in the Broughton Archipelago.

The present study demonstrated patterns in the distribution of the prevalence of adult *L. salmonis*, adult *C. clemensi* and immature lice stages on pink and chum salmon that were associated with size of the salmon, and with salinity and temperature. Tully & Nolan (2002) describe numerous co-occurring variables including the location(s), magnitude and timing of the sources of infection and oceanographic features that aid in the survival and distribution of planktonic sea lice stages. A thorough examination of the epizootiology of *L. salmonis* and *C. clemensi* in British Columbia (BC) that considers all these factors has previously not been undertaken. Recently, the distribution of sea lice-infected juvenile pink and

chum salmon within a limited area of the Broughton Archipelago was hypothesized to reflect the role of active salmon farms as sole sources of *L. salmonis* infection (Morton et al., 2004). In that study, juvenile pink and chum salmon were dip-netted over 10 weeks near and distant from farm sites containing salmon with unknown numbers of lice in their second year at sea. The exposed sites lay in zones F, G and H whereas the unexposed sites lay within zones F, J and K, as described in the present study. Mean abundances of all stages of *L. salmonis* on juvenile salmon (numbers of each species were not given) from exposed and unexposed sites were 6.78 and 0.81, respectively. Variations in sea lice abundance were shown to be not significantly associated with temperature and salinity however an effect of salmon size was not reported (Morton et al. 2004). A comparison of abundance data from Morton et al. (2004) and the present study, in which the abundance of all caligid copepods did not exceed 1.9 in any zone, suggests that the abundances of lice on pink and chum juveniles in this area were lower in 2003 compared with 2002. While more work is needed to understand inter-annual variations in sea lice infections on juvenile salmon, apparent differences in abundances between these studies may also be due to differences in sampling gear and sites and to the timing and size of samples. The present observations suggest inter-annual differences in the prevalence and possibly the abundance of sea lice in this area will reflect differences in temperature, salinity and the number, size and distribution of outmigrating juvenile salmon.

The scope of the present study did not include the effects of temporal and spatial variations in sources of infections on the prevalence of sea lice infections. The relatively low occurrence of gravid female *L. salmonis* however, suggests that during the study period, juvenile salmon were not yet capable of contributing significantly to the transmission of this species. Two alternative, but not mutually exclusive hypothetical reservoirs of infection include more mature wild salmonids that inhabit and overwinter in nearshore habitats and farmed salmonids, mainly Atlantic salmon. While certain populations of wild chinook salmon (*Oncorhynchus tshawytscha*) are known to migrate to sea in their first year and overwinter along coastal BC (Healey 1991), there are few data on their abundances in the study area. Similarly, coastally orientated populations of anadromous Dolly Varden char and cutthroat trout (Scott and Crossman 1973) are potential hosts. The importance of natural reservoirs of *L. salmonis* has been explored in two recent studies that focused on adult and juvenile salmon in the study area and adjacent coastal areas of British Columbia (R. Beamish, personal communication) and more widely from the coast of Oregon to Alaska (M. Trudel, personal communication). These studies have provided qualitative and quantitative information showing that overwintering, coastally distributed chinook and other species are hosts to *L. salmonis*. It is intuitive that a more detailed knowledge of the role of Pacific salmon as hosts of reproductively active *L. salmonis* is required in coastal waters throughout the year. The second hypothesis is that captive (farmed) species, mainly Atlantic salmon (*Salmo salar*), that are known to host infections with *L. salmonis* in BC and

elsewhere (Johnson and Margolis 1993, Wootten et al. 1982), serve as a source of infection for juvenile Pacific salmon. While this argument has been advanced (Morton et al. 2004), there are few data yet publicly available on levels of lice on farmed salmon in BC that would permit an objective test of this hypothesis. The distributions and magnitudes of the sources of infection should be examined and the relative contribution from captive and wild salmonids to a total pool of planktonic lice stages determined (Tully & Whelan, 1993) as these will undoubtedly vary from year to year. Understanding the role of salmon farms in the epizootiology of *L. salmonis* and *C. clemensi* in this region requires more focused, collaborative study.

Comparisons of apparent growth rates and condition factors between infected and uninfected pink and chum salmon were used to estimate the impact of sea lice infection. Condition factor was similar or higher on infected compared with uninfected salmon. Condition factor was previously (Bjørn and Finstad 1997, Grimnes and Jakobsen 1996) shown to be reduced among moribund sea trout and Atlantic salmon following laboratory exposures to lethal levels of *L. salmonis*. Our results suggested that levels of sea lice infections observed in the Broughton Archipelago in 2003 were not sufficiently severe to affect apparent growth or condition factor of juvenile pink and chum salmon. While it is possible that severely affected fish had been removed from the population prior to sampling, our data included fish with up to 12 (on pink) or 25 (on chum) lice. The lengths and weights of these heavily infected individuals aligned tightly with the length - weight regressions of the entire population for both species (data not shown). Similar observations on growth rates and condition factor were made for infections with non-motile and motile stages of *Lepeophtheirus salmonis* and *Caligus clemensi*. However, the prevalence of motile *L. salmonis* began to increase on pink salmon in the latter half of the study and it is possible that impact from these stages would only have been evident with continued sampling. The estimate of condition factor used here did not account for the contribution of water to body mass (Sutton et al. 2000) and other estimators of condition such as total energy content or haematological parameters that may be more useful indicators of disease impact (Rand and Cone 1990) should be considered in future studies. As well, we did not estimate more subtle physiological consequences of infection, such as swimming performance (Wagner et al. 2003), and the possible differential survival of infected and uninfected salmon. By definition, host fish will incur some physiological cost associated with a parasite infection. The extent and consequences of the physiological costs associated with the relatively low prevalence and intensities of sea lice stages observed in this study are unknown. Furthermore, the relative impact of sea lice and the many other parasites to which Pacific salmon are exposed during their life histories (Arthur and Margolis 1979, McDonald and Margolis 1995) will be difficult to predict. The extent, timing and mechanisms of mortality among juvenile pink and chum salmon from emergence to early marine rearing is poorly understood. Parker (1971) estimated that mortality among pink salmon ranged from 55% to 77% during the first 40 days of sea life and cited

predation by juvenile coho as the main cause of mortality. Mortality among juvenile chum salmon following marine migration is also thought to be mainly due to predation, with survival rates similar to or lower than those of pink salmon (Salo 1991). Regardless, survival to spawning among Pacific salmon is typically less than 5% and very little is known about when and by what mechanism these fish are lost. Specifically, there are little data documenting the extent to which caligid copepods contribute to marine mortality of Pacific salmon. Parker (1968) reported damage to skin and fins of juvenile pink salmon infected with *C. clemensi* in Burke Channel, BC. The latter author reported prevalence greater than 10% in some samples. The tissue damage described in the latter report may have contributed directly or indirectly to mortality but this was not documented. Physical damage to juvenile salmon associated with sea lice was not observed in the present study. Poor growth during early marine life is associated with reduced marine survival of coho salmon (Beamish et al. 2004). If similar relationships are valid for pink and chum salmon, then our data suggested that sea lice infections observed in 2003 would not significantly contribute to marine mortality in these species. The possibility that *L. salmonis* infections have an impact on the survival of wild salmonid populations is an area of considerable controversy however, and has been debated vigorously in regions surrounding the north Atlantic with no clear consensus (Pike and Wadsworth (1999). Further research is required to determine the extent to which sea lice impact juvenile Pacific salmon along with the inter-annual variation of possible impacts.

In summary, sea lice infections were observed on juvenile pink and chum salmon and on three-spine sticklebacks throughout the study area and, with the exception of week 1, throughout the duration of the study. At least four species of lice were observed: *Lepeophtheirus salmonis* on the salmon; *Caligus clemensi* on the salmon and sticklebacks; a second, unidentified species of *Lepeophtheirus* on sticklebacks and a fourth species, *Lepeophtheirus hospitalis* on herring (*Clupea pallasi*) collected in this study (data not shown). The hypothesis that sea lice are uniformly distributed within this region was rejected and several biological and environmental variables were also shown to be heterogeneously distributed throughout the study. These included salmon size (length and mass), salinity and temperature. Furthermore, logistic regression models showed that the probabilities of all categories of infection were positively associated with salmon size, salinity and temperature, as predicted from earlier studies. There was no evidence to support a hypothesis that the infection categories tested (motile *Lepeophtheirus*, motile *Caligus*, combined non-motile stages of both species) affected the size or condition factor of juvenile pink or chum salmon. Given the demonstrated biological and oceanographic complexities of this region, further studies are warranted to accurately document inter-annual variation. Furthermore, questions relating to fundamental features of sea lice epizootiology (for example source and impact) will benefit from collaborative research programs involving the stakeholders that share this coastal region.

RECOMMENDATIONS

1. To initiate and coordinate field and laboratory studies to better understand the impact of sea lice and other infectious diseases on wild juvenile salmon. Field studies should be linked with objective measures of impact including strength of the subsequent spawning population. Such studies should include but not be limited to:
    - surveys of the abundance, distribution, growth rate, condition and susceptibility of juvenile salmon;
    - oceanographic parameters associated with salmon migratory corridors including temperature, salinity and productivity;
    - knowledge of the seasonal abundance and distribution of wild and captive sources of sea lice.

2. To establish mechanisms for sharing relevant disease and environmental information between industry and DFO for example by initiating collaborative research programs to better understand local factors influencing prevalence, distribution and sources of sea lice infections on juvenile salmon

3. To initiate studies to improve knowledge of the morphological characteristics of the copepodid and chalimus stages of the *Lepeophtheirus* species parasitic on non-salmonid fishes in BC.

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REFERENCES

Anonymous (2002). 2002 Advisory: the protection of Broughton Archipelago pink salmon stocks. Pacific Fisheries Resource Conservation Council, Vancouver, British Columbia (http://fish.bc.ca/reports/pfrcc_broughton_advisory_full.pdf)

Beamish RJ, Mahnken C, Neville CM. (2004). Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. Transactions of the American Fisheries Society 133: 26-33.

Berger VY (1970). Influence of sea water of different salinities on *Lepeophtheirus salmonis* (Krøyer) a parasite of salmon. Parazitologiya 4: 136-138.

Bjørn PA, B Finstad (1997). The physiological effects of salmon lice infection on sea trout smolts. Nordic Journal of Freshwater Research 73: 60-72.

Costello MJ (1993). Review of methods to control sea lice (Caligidae: Crustacea) infestations on salmon (*Salmo salar*) farms. In: Pathogens of Wild and Farmed Fish: Sea Lice. GA Boxshall and D Defay (eds). Ellis Horwood, Chichester, UK. pp 219-252.

Fast MD, NW Ross, A. Mustafa, DE Sims, SC Johnson, GA Conboy, DJ Speare, G. Johnson, JF Burka (2002). Susceptibility of rainbow trout *Oncorhynchus mykiss*, Atlantic salmon *Salmo salar* and coho salmon *Oncorhynchus kisutch* to experimental infection with sea lice *Lepeophtheirus salmonis*. Diseases of Aquatic Organisms 52: 57-68.

Grimnes A, PJ Jakobsen (1996). The physiological effects of salmon lice infection on post-smolt of Atlantic salmon. Journal of Fish Biology 48: 1179-1194.

Hahnenkamp L, HJ Fyhn (1985). The osmotic response of salmon louse, *Lepeophtheirus salmonis* (Copepoda: Caligidae), during the transition from sea water to fresh water. Journal of Comparative Physiology B155: 357-365.

Hanley J.A. 1989. Receiver operating characteristic (ROC) methodology: the state of the art. Critical Reviews in Diagnostic Imaging 29: 307-335.

Hargreaves NB, D Herriot, V Palermo (2004). Pink Salmon Action Plan: Abundance and distribution of juvenile salmon and other fish caught in the Broughton Archipelago, Knight Inlet and Muchalat Inlet, B.C. in 2003. PSARC Working Paper H2004-02.

Healey MC (1991). Life history of chinook salmon (*Oncorhynchus tshawytscha*). In: Pacific Salmon Life Histories. C Groot, L Margolis (eds). UBC Press, Vancouver. pp 313-393.

Heard WR (1991). Life history of pink salmon (*Oncorhynchus gorbuscha*). In: Pacific Salmon Life Histories. C Groot, L Margolis (eds). UBC Press, Vancouver. pp 121-230.

Heuch PA (1995) Experimental evidence for aggregation of salmon louse copepodids (Lepeophtheirus salmonis) in step salinity gradients. Journal of the Marine Biological Association of the United Kingdom 75: 927-939.

Heuch PA, A Parsons, K Boxaspen (1995). Diel vertical migration: a possible host-finding mechanism in salmon louse (*Lepeophtheirus salmonis*) copepodids? Canadian Journal of Fisheries and Aquatic Sciences 52: 681-689.

Heuch PA, HE Karlsen (1997) Detection of infrasonic water oscillations by copepodids of *Lepeophtheirus salmonis* (Copepoda: Caligidae). Journal of Plankton Research 19: 735-747.

Ingvarsdóttir A, MA Birkett, I Duce, RL Genna, W Mordue, JA Pickett, LJ Wadhams, AJ Mordue (2002). Semiochemical strategies for sea louse control: host location cues. Pest Management Science 58: 537-545.

Johnson SC (1998) Crustacean parasites. In: Diseases of Seawater Netpen-Reared Salmonid Fishes. ML Kent, TT Poppe (eds). Fisheries and Oceans Canada. pp 80-97.

Johnson SC, LJ Albright (1991a). *Lepeophtheirus cuneifer* Kabata, 1974 (Copepoda: Caligidae) from seawater-reared rainbow trout, *Oncorhynchus mykiss*, and Atlantic salmon, *Salmo salar*, in the Strait of Georgia, British Columbia, Canada. Canadian Journal of Zoology 69: 1414-1416.

Johnson SC, LJ Albright (1991b). The developmental stages of *Lepeophtheirus salmonis* (Kroyer, 1837) (Copepoda: Caligidae) under laboratory conditions. Canadian Journal of Zoology 69: 929-950.

Johnson SC, LJ Albright (1991c). Development, growth and survival of *Lepeophtheirus salmonis* (Copepoda: Caligidae) under laboratory conditions. Journal of the Marine Biological Association of the UK 71: 425-436.

Johnson SC, LJ Albright (1992). Comparative susceptibility and histopathology of the responses of naïve coho, Atlantic and chinook salmon to experimental

infection with *Lepeophtheirus salmonis* (Copepoda: Caligidae). Diseases of Aquatic Organisms 14: 179-193.

Johnson SC, L Margolis (1993). The efficacy of ivermectin for the control of sea lice on sea-farmed Atlantic salmon. Diseases of Aquatic Organisms 17: 107-112.

Kabata Z (1972). Developmental stages of *Caligus clemensi* (Copepoda: Caligidae) from fishes of British Columbia. Journal of the Fisheries Research Board of Canada 29: 1571-1593.

Kabata Z (1973). The species of *Lepeophtheirus* (Copepoda: Caligidae) from fishes of British Columbia. Journal of the Fisheries Research Board of Canada 30: 729-759.

Kabata Z (1974). *Lepeophtheirus cuneifer* sp.nov. (Copepoda: Caligidae), a parasite of fishes from the Pacific coast of North America. Journal of the Fisheries Research Board of Canada 31: 43-47.

Margolis L, GW Esch, JC Holmes, AM Kuris, GA Schad (1982). The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). Journal of Parasitology 68: 131-133.

Margolis L, JR Arthur (1975). Synopsis of the parasites of fishes of Canada. Bulletin of the Fisheries Research Board of Canada, Number 199. Ottawa. 269 pages.

McDonald TE, L Margolis (1995). Synopsis of the parasites of fishes of Canada (1978-1993). Canadian Special Publication of Fisheries and Aquatic Sciences No. 122. National Research Council of Canada, Ottawa. 265 pages.

Morton A, R Routledge, C Peet, A Ladwig (2004). Sea lice (*Lepeophtheirus salmonis*) infection rates on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in the nearshore marine environment of British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 61: 147-157.

Mustafa A, C MacWilliams, N Fernandez, K Matchett, GA Conboy, JF Burka (2000). Effects of sea lice (*Lepeophtheirus salmonis* Kroyer, 1837) infestation on macrophage functions in Atlantic salmon (Salmo salar L.). Fish and Shellfish Immunology 10: 47-59.

Nagasawa K, Y Ishda, M Ogura, K Tadokoro, K Hiramatsu (1993). The abundance and distribution of *Lepeophtheirus salmonis* (Copepoda: Caligidae) on six

species of Pacific salmon in offshore waters of the North Pacific Ocean and Bering Sea. In: Pathogens of Wild and Farmed Fish: Sea Lice. GA Boxshall and D Defay (eds). Ellis Horwood, Chichester, UK. pp 166-178.

Nagasawa K (2001). Annual changes in the population size of the salmon louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) on high-seas Pacific salmon (Oncorhynchus spp.), and relationship to host abundance. Hydrobiologia 453/454: 411-416.

Neilson JD, GH Geen, D Bottom (1985). Estuarine growth of juvenile chinook salmon (*Oncorhynchus tshawytscha*) as inferred from otolith microstructure. Canadian Journal of Fisheries and Aquatic Sciences 42: 899-908.

Parker RR (1968). Mortality of juvenile pink salmon in central British Columbia coastal waters. Fisheries Research Board of Canada Manuscript Report Series, No. 956. 5 pages.

Parker RR, L Margolis (1964). A new species of parasitic copepod, *Caligus clemensi* sp. nov. (Caligoida: Caligidae), from pelagic fishes in the coastal waters of British Columbia. Journal of the Fisheries Research Board of Canada 21: 873-889.

Pike AW, SL Wadsworth (1999). Sealice on salmonids: their biology and control. Advances in Parasitology 44: 233-330.

Rand TG DK Cone (1990) Effects of *Ichthyophonus hoferi* on condition indices and blood chemistry of experimentally infected rainbow trout (*Oncorhynchus mykiss*). Journal of Wildlife Diseases 26: 323-328.

Revie CW, G Gettinby, JW Treasurer, GH Rae, N Clark (2002). Temporal, environmental and management factors influencing the epidemiological patterns of sea lice (*Lepeophtheirus salmonis*) infestations on farmed Atlantic salmon (*Salmo salar*) in Scotland. Pest Management Science 58: 576-594.

Salo EO (1991). Life history of chum salmon (*Oncorhynchus keta*). In: Pacific Salmon Life Histories. C Groot, L Margolis (eds). UBC Press, Vancouver. pp 233-309.

Schram TA (1993). Supplementary descriptions of the developmental stages of *Lepeophtheirus salmonis* (Kroyer, 1837) (Copepoda: Caligidae). In: Pathogens of Wild and Farmed Fish: Sea Lice. GA Boxshall and D Defay (eds). Ellis Horwood, Chichester, UK. pp 30-50.

Scott WB, EJ Crossman. 1973. Freshwater fishes of Canada. Bulletin 184, Fisheries Research Board of Canada, Ottawa, 966 p.

Stephen C (1991). Outbreak investigations in netpens. In: Diseases of Seawater Netpen-Reared Salmonid Fishes. ML Kent, TT Poppe (eds). Fisheries and Oceans Canada. pp 3-5.

Sutton SG, TP Bult, RL Haedrich (2000). Relationships among fat weight, body weight, water weight, and conditions factors in wild Atlantic salmon parr. Transactions of the American Fisheries Society 129: 527-538.

Tucker CS, C Sommerville, R Wootten (2000). The effect of temperature and salinity on the settlement and survival of copepodids of *Lepeophtheirus salmonis* (Kroyer, 1837) on Atlantic salmon, *Salmo salar* L. Journal of Fish Diseases 23: 309-320.

Tully O (1989). The succession of generations and growth of the caligid copepod *Caligus elongatus* and *Lepeophtheirus salmonis* parasitizing farmed Atlantic salmon smolts (*Salmo salar* L.). Journal of the Marine Biological Association of the UK 69: 279-287.

Tully O, DT Nolan (2002). A review of the population biology and host-parasite interactions of the sea louse *Lepeophtheirus salmonis* (Copepoda: Caligidae). Parasitology 124: S165-S182.

Wagner GN, RS McKinley (2004). Anaemia and salmonid swimming performance: the potential effects of sub-lethal sea lice infection. Journal of Fish Biology 64: 1027-1038.

Wagner GN, RS McKinley, PA Bjørn, B Finstad (2003). Physiological impact of sea lice on swimming performance of Atlantic salmon. Journal of Fish Biology 62:1000-1009.

Wootten R, JW Smith, EA Needham (1982). Aspects of the biology of the parasitic copepods *Lepeophtheirus salmonis* and *Caligus elongatus* on farmed salmonids and their treatment. Proceedings of the Royal Society of Edinburgh 81B: 185-197.

Table 1. Parasitic copepods of the family Caligidae reported from marine fishes off British Columbia (from Margolis and Arthur 1979 and McDonald and Margolis 1995)

Parasite species	Host species	Common Name
Caligus clemensi	*Clupea pallasi* *Gasterosteus aculeatus* *Oncorhynchus keta* *Oncorhynchus kisutch* *Oncorhynchus mykiss* *Oncorhynchus nerka* *Oncorhynchus tshawytscha* *Oncorhynchus gorbuscha* *Salmo salar* *Hexagrammos* sp. *Hydrolagus colliei* *Sebastes caurinus* *Sebastes* sp. *Theragra chalcogramma*	Pacific herring 3-spine stickleback chum salmon coho salmon steelhead sockeye salmon chinook salmon pink salmon Atlantic salmon greenling spotted ratfish copper rockfish rockfish walleye Pollock
Caligus macarovi	*Cololabis saira*	Pacific saury
Caligus sp.	*Merlucius productus*	Pacific hake
Lepeophtheirus bifidus	*Pleuronectes vetulus* *Pleuronichthys decurrens* *Pleuronectes bilineatus*	English sole curlfin sole rock sole
Lepeophtheirus breviventris	*Ophiodon elongatus*	lingcod
Lepeophtheirus cuneifer	*O. mykiss* *S. salar*	steelhead Atlantic salmon
Lepeophtheirus hospitalis	*Gadus macrocephalus* *P. bilineatus* *P. vetulus* *Platichthys stellatus* *Pleuronichthys coenosus* *Hexagrammos* sp.	Pacific cod rock sole English sole starry flounder c-o sole greenling

Parasite species	Host species	Common Name
Lepeophtheirus nanaimoensis	*Citharichthys sordidus*	unspecified flounder Pacific sand dab
Lepeophtheirus oblitus	*Hexagrammos decagrammus* *Hexagrammos stelleri* *Sebastes alutus* *S. caurinus* *Sebastes helvomaculatus* *Sebastes maliger* *Sebastes* sp.	kelp greenling whitespotted greenling Pacific ocean perch copper rockfish rosethorn rockfish quillback rockfish rockfish
Lepeophtheirus parvicruris	*P. stellatus*	starry flounder
Lepeophtheirus parviventris	*Anoplopoma fimbria* *Enophrys bison* *Eopsetta jordani* *G. macrocephalus* *H. decagrammus* *P. bilineatus* *Myoxocephalus polyacanthocephalus* *Raja binoculata* *Raja rhina* *Scorpaenichthys marmoratus* *Sebastes pinniger* *Xiphister atropurpureus* *T. chalcogramma*	sablefish buffalo sculpin petrale sole Pacific cod kelp greenling rock sole great sculpin big skate longnose skate cabezon canary rockfish black prickleback walleye pollock
Lepeophtheirus paulus	*Sebastes diploproa* *Sebastes flavidis* *S. maliger* *Sebastes nigrocinctus* *Sebastes ruberrimus* *T. chalcogramma*	splitnose rockfish yellowtail rockfish quillback rockfish tiger rockfish yelloweye rockfish walleye Pollock
Lepeophtheirus pravipes	*Hippoglossus stenolepis* *O. elongatus* *R. binoculata*	Pacific halibut lingcod big skate
Lepeophtheirus	*Acipenser*	white sturgeon

Parasite species	Host species	Common Name
salmonis	*transmontanus*	
	Ammodytes hexapterus	Pacific sand lance
	O. elongatus	lingcod
	O. gorbuscha	pink salmon
	O. keta	chum salmon
	O. kisutch	coho salmon
	O. mykiss	steelhead
	O. nerka	sockeye salmon
	O. tshawytscha	chinook salmon
	S. salar	Atlantic salmon
	Oncorhynchus clarki	cutthroat trout
Lepeophtheirus sp.	*E. jordani*	petrale sole
	G. macrocephalus	Pacific cod
	G. aculeatus	3-spine stickleback
	M. productus	Pacific hake
	P. vetulus	English sole
	S. maliger	quillback rockfish
	T. chalcogramma	walleye pollock

Table 2. Orders and species of fish that are host to caligid copepods in coastal British Columbia (from Margolis and Arthur 1979 and McDonald and Margolis 1995)

RAJIFORMES
- *Raja binoculata*
- *Raja rhina*

CHIMAERIFORMES
- *Hydrolagus colliei*

AC[illegible]IFORMES
- [illegible]*montanus*

CL[illegible]

GAS[illegible]
- G[illegible]*aculeatus*

SALMONIFORMES
- *Oncorhynchus keta*
- *Oncorhynchus kisutch*
- *Oncorhynchus mykiss*
- *Oncorhynchus nerka*
- *Oncorhynchus tshawytscha*
- *Oncorhynchus gorbuscha*
- *Oncorhynchus clarki*
- *Salmo salar*

GADIFORMES
- *Theragra chalcogramma*
- *Gadus macrocephalus*
- *Merlucius productus*

ATHERINIFORMES
- *Cololabis saira*

PLEURONECTIFORMES
- *Pleuronectes vetulus*
- *Pleuronichthys decurrens*
- *Pleuronectes bilineatus*
- *Platichthys stellatus*
- *Pleuronichthys coenosus*
- *Citharichthys sordidus*
- *Hippoglossus stenolepis*
- *Eopsetta jordani*

SCORPAENIFORMES
- *Myoxocephalus polyacanthocephalus*
- *Scorpaenichthys marmoratus*
- *Enophrys bison*
- *Hexagrammos decagrammus*
- *Hexagrammos stelleri*
- *Sebastes alutus*
- *Sebastes helvomaculatus*
- *Sebastes maliger*
- *Sebastes pinniger*
- *Sebastes diploproa*
- *Sebastes flavidis*
- *Sebastes nigrocinctus*
- *Sebastes ruberrimus*
- *Sebastes caurinus*
- *Anoplopoma fimbria*
- *Ophiodon elongatus*

PERCIFORMES
- *Xiphister atropurpureus*
- *Ammodytes hexapterus*

Table 3. Number of chum salmon examined in the laboratory

Weeks	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	All
A	0	5	7	0	0	0	0	0	0	0	0	0	0	0	0	12
B	0	68	34	136	41	109	127	151	154	170	120	120	121	129	42	1522
C	0	66	57	44	6	38	32	49	177	72	60	20	47	61	18	747
D	20	47	4	96	69	98	89	30	163	15	92	73	76	130	76	1078
E	0	30	25	37	2	24	0	21	5	0	1	25	21	57	26	274
F	68	57	140	96	121	78	74	119	145	125	153	74	159	169	113	1691
G	60	74	117	171	156	94	158	97	134	86	38	30	42	31	73	1361
H	24	21	60	135	99	57	156	111	109	67	78	130	90	89	214	1440
I	4	2	60	84	139	57	104	76	84	120	76	4	171	42	22	1045
J	0	0	133	6	92	188	73	65	133	113	104	53	173	88	72	1293
K	34	8	3	44	36	40	60	19	151	118	47	10	72	106	60	808
All	210	378	640	849	761	783	873	738	1255	886	769	539	972	902	716	11271

Table 4. Number of pink salmon examined in the laboratory

Weeks	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	All
B	0	30	6	68	6	60	31	52	66	35	13	47	87	30	26	557
C	0	22	27	29	1	34	4	35	121	81	90	69	66	77	0	656
D	5	39	2	86	45	43	19	44	127	23	75	60	135	166	99	968
E	0	3	14	29	0	32	0	16	0	1	0	14	13	31	46	199
F	46	10	94	68	22	15	19	34	104	78	120	61	104	86	65	926
G	17	12	32	23	38	35	53	64	13	55	30	32	22	7	12	445
H	36	17	64	64	49	8	90	86	58	57	49	111	63	36	135	923
I	5	3	82	27	145	62	84	39	62	59	38	0	71	2	1	680
J	0	0	120	3	134	167	21	19	16	1	6	3	34	6	27	557
K	37	32	2	142	53	42	42	50	251	157	169	132	139	221	58	1527
All	146	168	443	539	493	498	363	439	818	547	590	529	734	662	469	7438

Table 5. Number of 3-spine sticklebacks examined in the laboratory

Weeks	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	All
B	0	15	51	1	23	29	18	0	7	6	36	12	8	44	58	308
C	0	1	2	1	22	12	15	18	15	9	21	24	60	75	41	316
D	1	29	0	1	91	33	12	50	37	100	30	28	61	12	8	493
E	0	0	0	0	0	2	0	0	0	20	1	0	0	32	0	55
F	3	4	16	0	34	3	12	6	10	24	85	105	81	2	67	452
G	1	37	9	2	0	2	9	2	10	3	46	32	55	2	15	225
H	1	1	2	9	3	0	2	0	4	32	19	43	6	2	23	147
I	0	1	14	0	1	0	2	1	3	17	31	30	71	88	81	340
J	0	0	2	0	0	1	2	1	5	62	24	17	84	116	42	356
K	0	1	2	3	0	0	1	0	2	10	32	0	32	6	34	123
All	6	89	98	17	174	82	73	78	93	283	325	291	458	379	369	2815

Table 6. Two-way analysis of variance and Tukey pair-wise comparison of chum salmon fork lengths (natural logarithmic transformation) within the Broughton Archipelago and Knight Inlet over weeks and consolidated areas.

ANOVA Table

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Zone	3	2.62966	0.876554	25.18826	0.000000e+000
Week	14	35.33963	2.524260	72.53593	0.000000e+000
Zone:Week	41	3.69410	0.090100	2.58907	4.951568e-007
Residuals	682	23.73369	0.034800		

95 % simultaneous confidence intervals for specified linear combinations, by the Tukey method (intervals excluding 0 are flagged by '****')

	Estimate	Std.Error	Lower Bound	Upper Bound	
ABCJ-DF	**-0.0995**	**0.0189**	**-0.14800**	**-0.0508**	****
ABCJ-EHK	-0.0255	0.0196	-0.07580	0.0249	
ABCJ-GI	0.0325	0.0216	-0.02310	0.0881	
DF-EHK	**0.0740**	**0.0205**	**0.02130**	**0.1270**	****
DF-GI	**0.1320**	**0.0223**	**0.07450**	**0.1900**	****
EHK-GI	0.0580	0.0229	-0.00101	0.1170	

Table 7. Two-way analysis of variance and Tukey pair-wise comparison of chum salmon mass (natural logarithmic transformation) within the Broughton Archipelago and Knight Inlet over weeks and consolidated areas.

ANOVA Table

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Zone	3	29.5480	9.84935	27.55000	0.000000e+000
Week	14	427.3782	30.52701	85.38831	0.000000e+000
Zone:Week	41	39.2714	0.95784	2.67921	1.755738e-007
Residuals	682	243.8205	0.35751		

95 % simultaneous confidence intervals for specified linear combinations, by the Tukey method (intervals excluding 0 are flagged by '****')

	Estimate	Std.Error	Lower Bound	Upper Bound	
ABCJ-DF	-0.325	0.0606	-0.4810	-0.1690	****
ABCJ-EHK	-0.104	0.0627	-0.2650	0.0578	
ABCJ-GI	0.101	0.0692	-0.0771	0.2800	
DF-EHK	0.221	0.0657	0.0523	0.3910	****
DF-GI	0.426	0.0716	0.2420	0.6110	****
EHK-GI	0.205	0.0734	0.0159	0.3940	****

Table 6. Two-way analysis of variance and Tukey pair-wise comparison of chum salmon fork lengths (natural logarithmic transformation) within the Broughton Archipelago and Knight Inlet over weeks and consolidated areas.

ANOVA Table

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Zone	3	2.62966	0.876554	25.18826	0.000000e+000
Week	14	35.33963	2.524260	72.53593	0.000000e+000
Zone:Week	41	3.69410	0.090100	2.58907	4.951568e-007
Residuals	682	23.73369	0.034800		

95 % simultaneous confidence intervals for specified linear combinations, by the Tukey method (intervals excluding 0 are flagged by '****')

	Estimate	Std.Error	Lower Bound	Upper Bound	
ABCJ-DF	-0.0995	0.0189	-0.14800	-0.0508	****
ABCJ-EHK	-0.0255	0.0196	-0.07580	0.0249	
ABCJ-GI	0.0325	0.0216	-0.02310	0.0881	
DF-EHK	0.0740	0.0205	0.02130	0.1270	****
DF-GI	0.1320	0.0223	0.07450	0.1900	****
EHK-GI	0.0580	0.0229	-0.00101	0.1170	

Table 7. Two-way analysis of variance and Tukey pair-wise comparison of chum salmon mass (natural logarithmic transformation) within the Broughton Archipelago and Knight Inlet over weeks and consolidated areas.

ANOVA Table

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Zone	3	29.5480	9.84935	27.55000	0.000000e+000
Week	14	427.3782	30.52701	85.38831	0.000000e+000
Zone:Week	41	39.2714	0.95784	2.67921	1.755738e-007
Residuals	682	243.8205	0.35751		

95 % simultaneous confidence intervals for specified linear combinations, by the Tukey method (intervals excluding 0 are flagged by '****')

	Estimate	Std.Error	Lower Bound	Upper Bound	
ABCJ-DF	-0.325	0.0606	-0.4810	-0.1690	****
ABCJ-EHK	-0.104	0.0627	-0.2650	0.0578	
ABCJ-GI	0.101	0.0692	-0.0771	0.2800	
DF-EHK	0.221	0.0657	0.0523	0.3910	****
DF-GI	0.426	0.0716	0.2420	0.6110	****
EHK-GI	0.205	0.0734	0.0159	0.3940	****

Table 8. Two-way analysis of variance and Tukey pair-wise comparison of pink salmon fork length (natural logarithmic transformation) within the Broughton Archipelago and Knight Inlet over weeks and consolidated areas.

ANOVA Table

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Zone	3	2.59838	0.866127	45.1289	0.000000e+000
Week	14	48.37812	3.455580	180.0503	0.000000e+000
Zone:Week	41	2.51207	0.061270	3.1924	8.384732e-010
Residuals	510	9.78807	0.019192		

95 % simultaneous confidence intervals for specified linear combinations, by the Tukey method (intervals excluding 0 are flagged by '****')

	Estimate	Std.Error	Lower Bound	Upper Bound	
ABCJ-DF	**-0.108000**	**0.0175**	**-0.1530**	**-0.0630**	********
ABCJ-EHK	-0.000888	0.0170	-0.0448	0.0430	
ABCJ-GI	-0.027500	0.0215	-0.0828	0.0278	
DF-EHK	**0.107000**	**0.0162**	**0.0656**	**0.1490**	********
DF-GI	**0.080700**	**0.0208**	**0.0272**	**0.1340**	********
EHK-GI	-0.026600	0.0204	-0.0791	0.0259	

Table 9. Two-way analysis of variance and Tukey pair-wise comparison of pink salmon mass (natural logarithmic transformation) within the Broughton Archipelago and Knight Inlet over weeks and consolidated areas.

ANOVA Table

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Zone	3	28.6960	9.56534	45.6578	0.000000e+000
Week	14	583.6111	41.68650	198.9805	0.000000e+000
Zone:Week	41	24.0201	0.58586	2.7964	7.687839e-008
Residuals	510	106.8452	0.20950		

95 % simultaneous confidence intervals for specified linear combinations, by the Tukey method (intervals excluding 0 are flagged by '****')

	Estimate	Std.Error	Lower Bound	Upper Bound	
ABCJ-DF	**-0.34400**	**0.0580**	**-0.493**	**-0.194**	********
ABCJ-EHK	-0.00877	0.0563	-0.154	0.136	
ABCJ-GI	-0.07000	0.0709	-0.253	0.113	
DF-EHK	**0.33500**	**0.0535**	**0.197**	**0.473**	********
DF-GI	**0.27400**	**0.0686**	**0.097**	**0.451**	********
EHK-GI	-0.06120	0.0673	-0.235	0.112	

Table 8. Two-way analysis of variance and Tukey pair-wise comparison of pink salmon fork length (natural logarithmic transformation) within the Broughton Archipelago and Knight Inlet over weeks and consolidated areas.

ANOVA Table

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Zone	3	2.59838	0.866127	45.1289	0.000000e+000
Week	14	48.37812	3.455580	180.0503	0.000000e+000
Zone:Week	41	2.51207	0.061270	3.1924	8.384732e-010
Residuals	510	9.78807	0.019192		

95 % simultaneous confidence intervals for specified linear combinations, by the Tukey method (intervals excluding 0 are flagged by '****')

	Estimate	Std.Error	Lower Bound	Upper Bound	
ABCJ-DF	-0.108000	0.0175	-0.1530	-0.0630	****
ABCJ-EHK	-0.000888	0.0170	-0.0448	0.0430	
ABCJ-GI	-0.027500	0.0215	-0.0828	0.0278	
DF-EHK	0.107000	0.0162	0.0656	0.1490	****
DF-GI	0.080700	0.0208	0.0272	0.1340	****
EHK-GI	-0.026600	0.0204	-0.0791	0.0259	

Table 9. Two-way analysis of variance and Tukey pair-wise comparison of pink salmon mass (natural logarithmic transformation) within the Broughton Archipelago and Knight Inlet over weeks and consolidated areas.

ANOVA Table

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Zone	3	28.6960	9.56534	45.6578	0.000000e+000
Week	14	583.6111	41.68650	198.9805	0.000000e+000
Zone:Week	41	24.0201	0.58586	2.7964	7.687839e-008
Residuals	510	106.8452	0.20950		

95 % simultaneous confidence intervals for specified linear combinations, by the Tukey method (intervals excluding 0 are flagged by '****')

	Estimate	Std.Error	Lower Bound	Upper Bound	
ABCJ-DF	-0.34400	0.0580	-0.493	-0.194	****
ABCJ-EHK	-0.00877	0.0563	-0.154	0.136	
ABCJ-GI	-0.07000	0.0709	-0.253	0.113	
DF-EHK	0.33500	0.0535	0.197	0.473	****
DF-GI	0.27400	0.0686	0.097	0.451	****
EHK-GI	-0.06120	0.0673	-0.235	0.112	

Table 10. Summary of infections with caligid copepods on juvenile chum and pink salmon and on 3-spine sticklebacks collected from the Broughton Archipelago and Knight Inlet, British Columbia in March to June, 2003.

	Chum	Pink	Stickleback
Total fish examined	11,271	7,438	2,815
Total infected	3,050	1,784	1,727
Total lice	6,648	2,952	10284
Prevalence (% infected)	27.1	24.0	61.3
Intensity (lice/infected fish)	2.18 (1 - 25)	1.65 (1 – 12)	5.95 (1 – 51)
Mean weight (g) (range)	1.96 (0.14 – 34.8)	1.65 (0.11 – 13.78)	3.39 (.07 – 10.75)
Mean fork length (mm) (range)	51.0 (28 – 138)	48.2 (23 – 110)	63.4 (19 – 98)

Table 11. Prevalence and mean abundance of sea lice on juvenile chum and pink salmon and on 3-spine sticklebacks

Host	No. Fish	Motile Lepeophtheirus		Motile Caligus		Total immature	
		% Infected	lice/fish	% Infected	lice/fish	% Infected	lice/fish
Chum	11,271	4.4	0.06	3.45	0.05	23.5	0.48
Pink	7,438	6.0	0.07	3.97	0.05	17.2	0.27
St'back	2,815	1.35	0.02	11.54	0.18	60.7	3.46

Table 12. Coefficients of generalized linear models of the prevalence of non-motile sea lice stage on chum and pink salmon collected over week categories (early, late) and four consolidated areas. |t-value| > 1.96 is significant.

Chum salmon

	Value	Std. Error	t value
(Intercept)	-1.1489339	0.2233368	**-5.144400**
AreaDF	2.1306895	0.2578837	**8.262210**
AreaEHK	2.6984404	0.2963298	**9.106206**
AreaGI	1.9381441	0.2769649	**6.997796**
week.cat	0.3641382	0.2095911	1.737374

Pink salmon

	Value	Std. Error	t value
(Intercept)	-1.963817	0.3303241	**-5.9451238**
AreaDF	2.159444	0.3483140	**6.1997041**
AreaEHK	3.426197	0.3700484	**9.2587809**
AreaGI	1.999998	0.3813026	**5.2451736**
Area.cat	0.248631	0.2524274	0.9849603

Table 13. Coefficients of generalized linear models of the prevalence of motile *Lepeophtheirus salmonis* on chum and pink salmon collected over week categories (early, late) and four consolidated areas. |t-value| > 1.96 is significant.

Chum salmon

	Value	Std. Error	t value
(Intercept)	-2.5996858	0.2823997	-9.205697
AreaDF	1.0512461	0.2702225	3.890298
AreaEHK	1.6133853	0.2729126	5.911730
AreaGI	0.6645394	0.3057540	2.173445
Week.cat	1.3765087	0.2324029	5.922940

Pink salmon

	Value	Std. Error	t value
(Intercept)	-3.6344472	0.4182517	-8.689617
AreaDF	1.7204550	0.3698044	4.652338
AreaEHK	2.4631731	0.3672937	6.706277
AreaGI	0.7519932	0.4500641	1.670858
week.cat	2.3122939	0.3203301	7.218473

Table 12. Coefficients of generalized linear models of the prevalence of non-motile sea lice stage on chum and pink salmon collected over week categories (early, late) and four consolidated areas. |t-value| > 1.96 is significant.

Chum salmon

	Value	Std. Error	t value
(Intercept)	-1.1489339	0.2233368	-5.144400
AreaDF	2.1306895	0.2578837	8.262210
AreaEHK	2.6984404	0.2963298	9.106206
AreaGI	1.9381441	0.2769649	6.997796
week.cat	0.3641382	0.2095911	1.737374

Pink salmon

	Value	Std. Error	t value
(Intercept)	-1.963817	0.3303241	-5.9451238
AreaDF	2.159444	0.3483140	6.1997041
AreaEHK	3.426197	0.3700484	9.2587809
AreaGI	1.999998	0.3813026	5.2451736
Area.cat	0.248631	0.2524274	0.9849603

Table 13. Coefficients of generalized linear models of the prevalence of motile *Lepeophtheirus salmonis* on chum and pink salmon collected over week categories (early, late) and four consolidated areas. |t-value| > 1.96 is significant.

Chum salmon

	Value	Std. Error	t value
(Intercept)	-2.5996858	0.2823997	-9.205697
AreaDF	1.0512461	0.2702225	3.890298
AreaEHK	1.6133853	0.2729126	5.911730
AreaGI	0.6645394	0.3057540	2.173445
Week.cat	1.3765087	0.2324029	5.922940

Pink salmon

	Value	Std. Error	t value
(Intercept)	-3.6344472	0.4182517	-8.689617
AreaDF	1.7204550	0.3698044	4.652338
AreaEHK	2.4631731	0.3672937	6.706277
AreaGI	0.7519932	0.4500641	1.670858
week.cat	2.3122939	0.3203301	7.218473

Table 14. Coefficients of generalized linear models of the prevalence of motile *Caligus clemensi* on chum and pink salmon collected over week categories and four consolidated areas. |t-value| > 1.96 is significant.

Chum salmon

	Value	Std. Error	t value
(Intercept)	-4.803781	0.4812168	-9.982571
AreaDF	2.565222	0.3806330	6.739359
AreaEHK	2.066874	0.3861044	5.353148
AreaGI	1.030143	0.4498826	2.289805
week.cat	2.363317	0.3699232	6.388670

Pink salmon

	Value	Std. Error	t value
(Intercept)	-4.55733674	0.6079794	-7.49587410
AreaDF	1.91611968	0.4095364	4.67875298
AreaEHK	1.30996902	0.3994870	3.27912795
AreaGI	-0.03694469	0.5914461	-0.06246502
Week.cat	2.86216534	0.5262591	5.43870045

Table 14. Coefficients of generalized linear models of the prevalence of motile *Caligus clemensi* on chum and pink salmon collected over week categories and four consolidated areas. |t-value| > 1.96 is significant.

Chum salmon

	Value	Std. Error	t value
(Intercept)	-4.803781	0.4812168	-9.982571
AreaDF	2.565222	0.3806330	6.739359
AreaEHK	2.066874	0.3861044	5.353148
AreaGI	1.030143	0.4498826	2.289805
week.cat	2.363317	0.3699232	6.388670

Pink salmon

	Value	Std. Error	t value
(Intercept)	-4.55733674	0.6079794	-7.49587410
AreaDF	1.91611968	0.4095364	4.67875298
AreaEHK	1.30996902	0.3994870	3.27912795
AreaGI	-0.03694469	0.5914461	-0.06246502
Week.cat	2.86216534	0.5262591	5.43870045

Table 15. Two-way analysis of variance and Tukey pair-wise comparison of surface sea water temperatures within the Broughton Archipelago and Knight Inlet over weeks and consolidated areas.

ANOVA Table

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
zone	3	158.026	52.6753	39.4001	0
week	10	3724.363	372.4363	278.5752	0
zone:week	30	281.133	9.3711	7.0094	0
Residuals	857	1145.751	1.3369		

95 % simultaneous confidence intervals for specified linear combinations, by the Tukey method (intervals excluding 0 are flagged by '****')

	Estimate	Std.Error	Lower Bound	Upper Bound	
ABCJ-DF	0.646	0.110	0.363	0.9280	****
ABCJ-EHK	0.776	0.105	0.506	1.0500	****
ABCJ-GI	-0.401	0.121	-0.712	-0.0905	****
DF-EHK	0.130	0.108	-0.149	0.4090	
DF-GI	-1.050	0.124	-1.370	-0.7290	****
EHK-GI	-1.180	0.120	-1.490	-0.8700	****

Table 16. Two-way analysis of variance and coefficients of linear model describing the sources of significant variation in sea surface salinity within the Broughton Archipelago and Knight Inlet over weeks and consolidated areas.

ANOVA Table

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
zone	3	9752.05	3250.685	109.4903	0.0000000000
week	6	4098.21	683.035	23.0061	0.0000000000
zone:week	18	1378.05	76.558	2.5787	0.0004569212
Residuals	381	11311.60	29.689		

Coefficients of linear model

	Value	Std. Error	t value	Pr(>|t|)
(Intercept)	16.6501	1.1617	14.3327	0.0000
zoneDF	7.8438	1.6623	4.7186	0.0000
zoneEHK	10.9876	1.7065	6.4387	0.0000
zoneGI	2.3433	2.0121	1.1646	0.2449
week10	-0.2208	1.7317	-0.1275	0.8986
week11	0.5425	1.6083	0.3373	0.7361
week12	-1.0547	1.8245	-0.5781	0.5636
week13	-5.0436	1.8628	-2.7075	0.0071
week14	-13.0993	2.1560	-6.0757	0.0000
week15	-9.2888	1.7065	-5.4432	0.0000
zoneDFweek10	1.4058	2.5037	0.5615	0.5748
zoneEHKweek10	0.2103	3.0838	0.0682	0.9457
zoneGIweek10	2.6435	2.9995	0.8813	0.3787
zoneDFweek11	1.3608	2.3586	0.5770	0.5643
zoneEHKweek11	0.4400	2.4756	0.1777	0.8590
zoneGIweek11	-2.0115	2.9299	-0.6865	0.4928
zoneDFweek12	-1.1842	2.5474	-0.4649	0.6423
zoneEHKweek12	1.2450	2.6480	0.4702	0.6385
zoneGIweek12	4.9020	3.6674	1.3366	0.1821
zoneDFweek13	0.1932	2.5236	0.0766	0.9390
zoneEHKweek13	-0.8210	2.6037	-0.3153	0.7527
zoneGIweek13	0.1769	3.2265	0.0548	0.9563
zoneDFweek14	14.6407	3.2099	4.5611	0.0000
zoneEHKweek14	9.8172	2.8402	3.4566	0.0006
zoneGIweek14	5.2572	3.1696	1.6586	0.0980
zoneDFweek15	5.9403	2.3823	2.4935	0.0131
zoneEHKweek15	0.9337	2.4747	0.3773	0.7062
zoneGIweek15	1.7618	2.9292	0.6015	0.5479

Table 16. Two-way analysis of variance and coefficients of linear model describing the sources of significant variation in sea surface salinity within the Broughton Archipelago and Knight Inlet over weeks and consolidated areas.

ANOVA Table

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
zone	3	9752.05	3250.685	109.4903	0.0000000000
week	6	4098.21	683.035	23.0061	0.0000000000
zone:week	18	1378.05	76.558	2.5787	0.0004569212
Residuals	381	11311.60	29.689		

Coefficients of linear model

	Value	Std. Error	t value	Pr(>|t|)
(Intercept)	16.6501	1.1617	14.3327	0.0000
zoneDF	7.8438	1.6623	4.7186	0.0000
zoneEHK	10.9876	1.7065	6.4387	0.0000
zoneGI	2.3433	2.0121	1.1646	0.2449
week10	-0.2208	1.7317	-0.1275	0.8986
week11	0.5425	1.6083	0.3373	0.7361
week12	-1.0547	1.8245	-0.5781	0.5636
week13	-5.0436	1.8628	-2.7075	0.0071
week14	-13.0993	2.1560	-6.0757	0.0000
week15	-9.2888	1.7065	-5.4432	0.0000
zoneDFweek10	1.4058	2.5037	0.5615	0.5748
zoneEHKweek10	0.2103	3.0838	0.0682	0.9457
zoneGIweek10	2.6435	2.9995	0.8813	0.3787
zoneDFweek11	1.3608	2.3586	0.5770	0.5643
zoneEHKweek11	0.4400	2.4756	0.1777	0.8590
zoneGIweek11	-2.0115	2.9299	-0.6865	0.4928
zoneDFweek12	-1.1842	2.5474	-0.4649	0.6423
zoneEHKweek12	1.2450	2.6480	0.4702	0.6385
zoneGIweek12	4.9020	3.6674	1.3366	0.1821
zoneDFweek13	0.1932	2.5236	0.0766	0.9390
zoneEHKweek13	-0.8210	2.6037	-0.3153	0.7527
zoneGIweek13	0.1769	3.2265	0.0548	0.9563
zoneDFweek14	14.6407	3.2099	4.5611	0.0000
zoneEHKweek14	9.8172	2.8402	3.4566	0.0006
zoneGIweek14	5.2572	3.1696	1.6586	0.0980
zoneDFweek15	5.9403	2.3823	2.4935	0.0131
zoneEHKweek15	0.9337	2.4747	0.3773	0.7062
zoneGIweek15	1.7618	2.9292	0.6015	0.5479

Table 17. Estimated coefficients (± std. error) for the logistic regression models for pink and chum salmon infected with non-motile and motile stages of *Caligus clemensi* and *Lepeophtheirus salmonis* (see Appendices 1 and 2)

Lice species/stage	Parameter	Effect	Chum Salmon	Pink Salmon
Motile *C. clemensi*	b_0	Constant	-16.17 ± 1.69	-17.21 ± 1.86
	b_{DF}	Zones D,F	1.813 ± 0.514	0
	b_{GI}	Zones G, I	0.7523 ± 0.5745	0
	b_{EHK}	Zones E,H,K	1.241 ± 0.540	0
	b_{weight}	Fish weight (g)	-0.1848 ± 0.0680	0
	b_{length}	Fish length (mm)	0.05907 ± 0.01365	0.05822 ± 0.00832
	$b_{temperature}$	Water temperature (°C)	0.3966 ± 0.0922	0.5251 ± 0.1046
	$b_{salinity}$	Salinity (‰)	0.1456 ± 0.0344	0.1636 ± 0.0371
Motile *L. salmonis*	b_0	Constant	-10.19 ± 1.26	-9.187 ± 1.043
	b_{DF}	Zones D,F	0.3370 ± 0.3821	1.078 ± 0.421
	b_{GI}	Zones G, I	0.6456 ± 0.4019	1.774 ± 0.474
	b_{EHK}	Zones E,H,K	0.8895 ± 0.3906	1.699 ± 0.424
	b_{weight}	Fish weight (g)	-0.1273 ± 0.0657	-0.1715 ± 0.1326
	b_{length}	Fish length (mm)	0.05045 ± 0.01251	0.06366 ± 0.01802
	$b_{temperature}$	Water temperature (°C)	0.1138 ± 0.0727	0
	$b_{salinity}$	Salinity (‰)	0.1130 ± 0.0253	0.0925 ± 0.0263
All immature stages	b_0	Constant	-9.165 ± 2.695	-7.565 ± 0.997
of both species	b_{DF}	Zones D,F	2.141 ± 0.902	2.507 ± 0.510
	b_{GI}	Zones G, I	2.101 ± 0.949	2.455 ± 0.567
	b_{EHK}	Zones E,H,K	2.597 ± 0.921	3.150 ± 0.507
	b_{weight}	Fish weight (g)	-0.5317 ± 0.3002	-0.4843 ± 0.1537
	b_{length}	Fish length (mm)	0.07798 ± 0.04443	0.02265 ± 0.01684
	$b_{temperature}$	Water temperature (°C)	-0.0226 ± 0.1229	0
	$b_{salinity}$	Salinity (‰)	0.1509 ± 0.0475	0.1210 ± 0.0270

Table 18. Analysis of variance of size and condition factor data for juvenile salmon infected with non-motile stages of *Lepeophtheirus* and *Caligus* (see Figures 32 and 35).

ANOVA (Weeks 6-15)

			Weight			Length			Condition		
Fish species	Effect	Num DF	MSE	F-ratio	Prob ≥ F	MSE	F-ratio	Prob ≥ F	MSE	F-ratio	Prob ≥ F
Chum	Lice	1	1.561	1.105	0.2947	439.9	6.765	0.0101	0.0421	7.4016	0.0072
	Week	9	40.97	29.01	0.0000	2278	35.03	0.0000	0.0780	13.70	0.0000
	Lice × Week	9	0.5837	0.4132	0.9268	17.37	0.2670	0.9825	0.0032	0.5568	0.8308
Pink	Lice	1	0.0867	0.0908	0.7636	2.859	0.0478	0.8273	0.0426	9.519	0.0024
	Week	9	28.83	30.19	0.0000	2377	39.74	0.0000	0.1223	27.322	0.0000
	Lice × Week	9	0.5929	0.6207	0.7780	19.64	0.8299	0.5897	0.0032	0.7160	0.6936

Estimated overall (all weeks) mean difference (infected - uninfected)

	Weight (g)		Length (mm)		Condition	
Fish species	Diff.	Std. Err.	Diff.	Std. Err.	Diff.	Std. Err.
Chum	0.015		1.88		0.025	
Pink	-0.20		-1.09		0.024	

Table 19. Analysis of variance of size and condition factor data for juvenile salmon infected with motile *Lepeophtheirus salmonis* (see Figures 33 and 36)

ANOVA (Weeks 6-15)

			Weight			Length			Condition		
Fish species	Effect	Num DF	MSE	F-ratio	Prob ≥ F	MSE	F-ratio	Prob ≥ F	MSE	F-ratio	Prob ≥ F
Chum	Lice	1	37.32	13.08	0.0004	2701	27.81	0.0000	0.0343	5.7161	0.0181
	Week	9	35.06	12.29	0.0000	1577	16.24	0.0000	0.0669	12.564	0.0000
	Lice × Week	9	0.8121	0.2846	0.9781	50.75	0.5226	0.8564	0.0044	0.8203	0.5983
Pink	Lice	1	6.6687	5.538	0.0200	853.1	11.80	0.0008	0.0007	0.1348	0.7140
	Week	9	29.729	24.69	0.0000	2032	28.11	0.0000	0.0854	17.349	0.0000
	Lice × Week	9	0.5055	0.4198	0.9228	30.17	0.4172	0.9242	0.0022	0.4376	0.9126

Estimated overall (all weeks) mean difference (infected - uninfected)

	Weight (g)		Length (mm)		Condition	
Fish species	Diff.	Std. Err.	Diff.	Std. Err.	Diff.	Std. Err.
Chum	1.02		8.52		0.037	
Pink	0.71		7.62		0.027	

Table 20. Analysis of variance of size and condition factor data for juvenile salmon infected with motile *Caligus clemensi* (see Figures 34 and 37).

ANOVA (Weeks 6-15)

			Weight			Length			Condition		
Fish species	Effect	Num DF	MSE	F-ratio	Prob ≥ F	MSE	F-ratio	Prob ≥ F	MSE	F-ratio	Prob ≥ F
Chum	Lice	1	10.29	3.990	0.0479	459	4.848	0.0295	0.0330	7.3621	0.0076
	Week	9	29.00	11.24	0.0000	1401	14.79	0.0000	0.0332	7.419	0.0000
	Lice × Week	9	1.927	0.7471	0.6652	90.46	0.9547	0.4808	0.0061	1.369	0.2089
Pink	Lice	1	10.38	9.422	0.0027	1043	16.62	0.0001	0.0166	3.419	0.0670
	Week	9	25.98	23.59	0.0000	1571	25.05	0.0000	0.0559	11.473	0.0000
	Lice × Week	9	0.4252	0.3861	0.9398	11.73	0.1870	0.9952	0.0030	0.6106	0.7859

Estimated overall (all weeks) mean difference (infected - uninfected)

	Weight (g)		Length (mm)		Condition	
Fish species	Diff.	Std. Err.	Diff.	Std. Err.	Diff.	Std. Err.
Chum	1.496		10.89		0.053	
Pink	1.30		11.84		0.051	

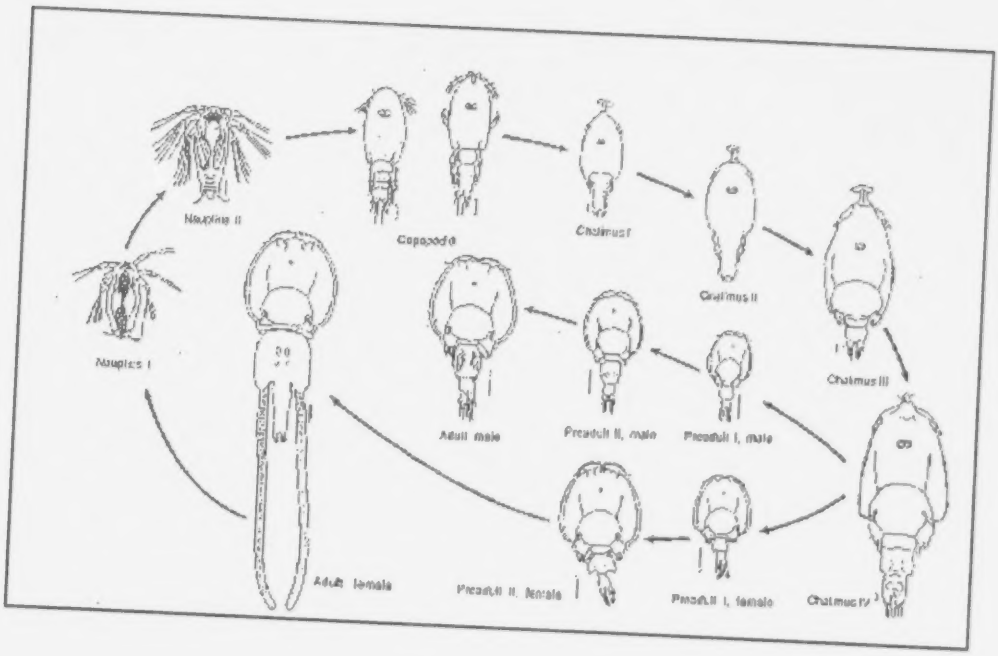

Figure 1. The life cycle of *Lepeophtheirus salmonis* (from Schram 1993).

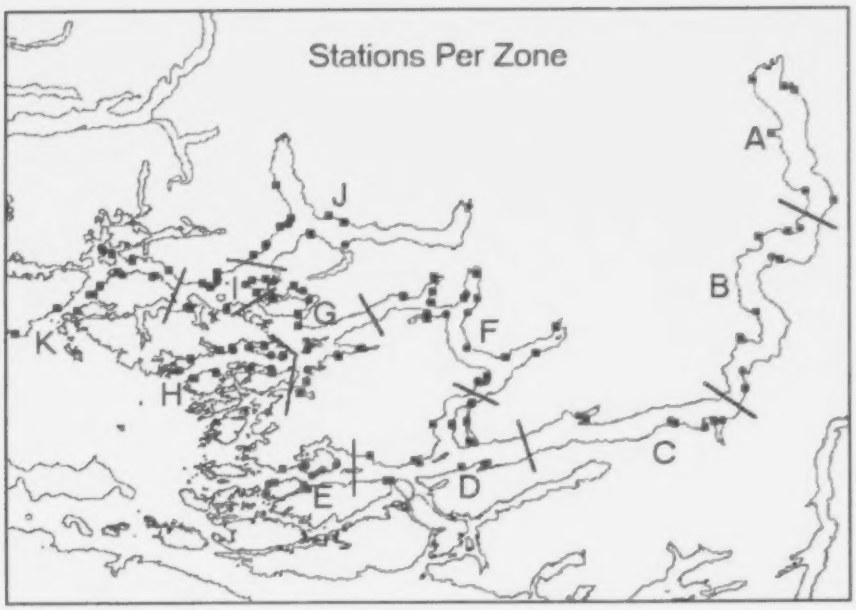

Figure 2. Map of the Broughton Archipelago and Knight Inlet areas of coastal British Columbia. Zones A to K were chosen as analytical units within the study area.

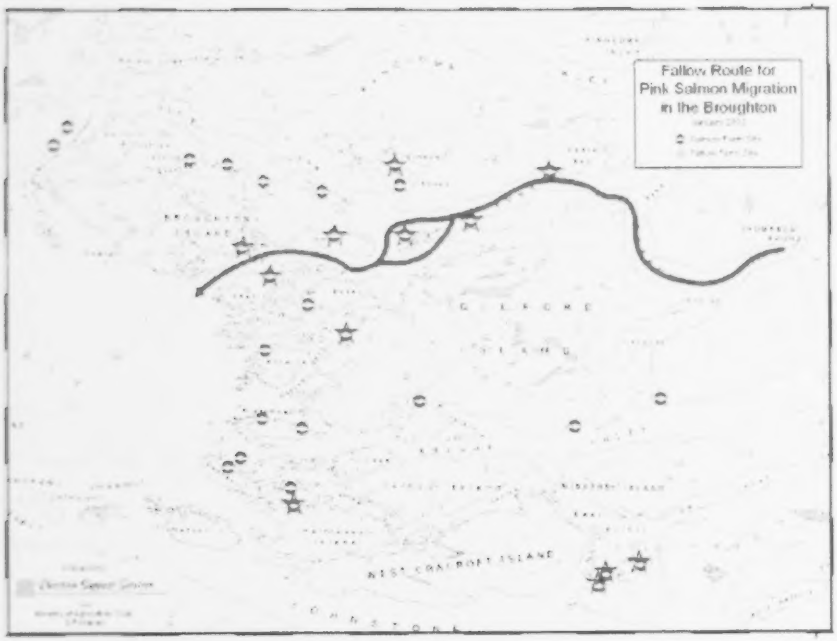

Figure 3. Map depicting BC Ministry of Agriculture, Food and Fisheries "Fallow Route for Pink Salmon Migration" in the Broughton". Salmon farms along this corridor were fallowed prior to and during the study period, as indicated. (from: http://www.agf.gov.bc.ca/fisheries/images/broughton_corridor.jpg)

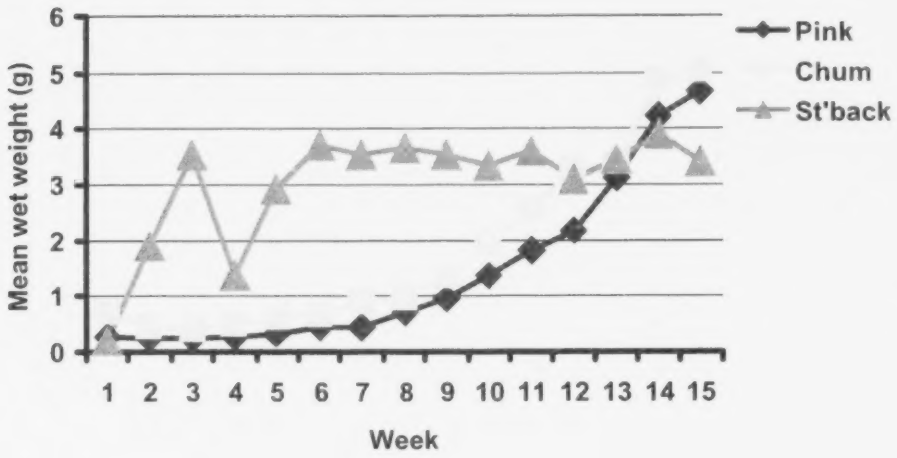

Figure 4. Weekly mean wet masses of juvenile pink and chum salmon and of 3-spine sticklebacks during the study period.

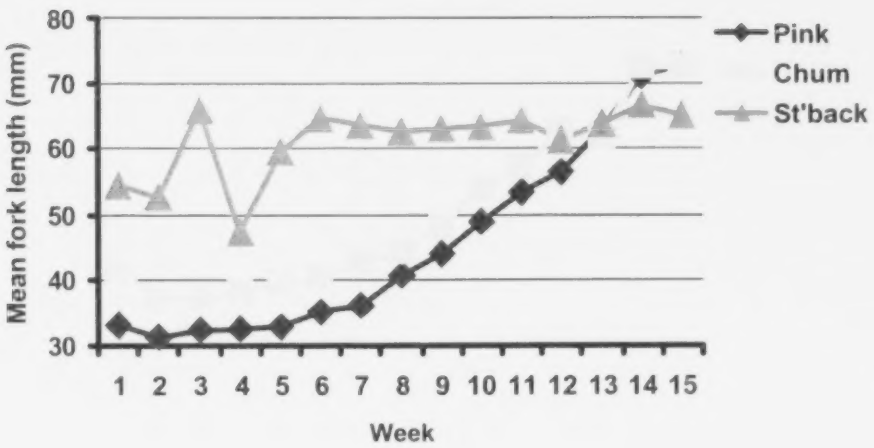

Figure 5. Weekly mean fork lengths of juvenile pink and chum salmon and of 3-spine sticklebacks during the study period.

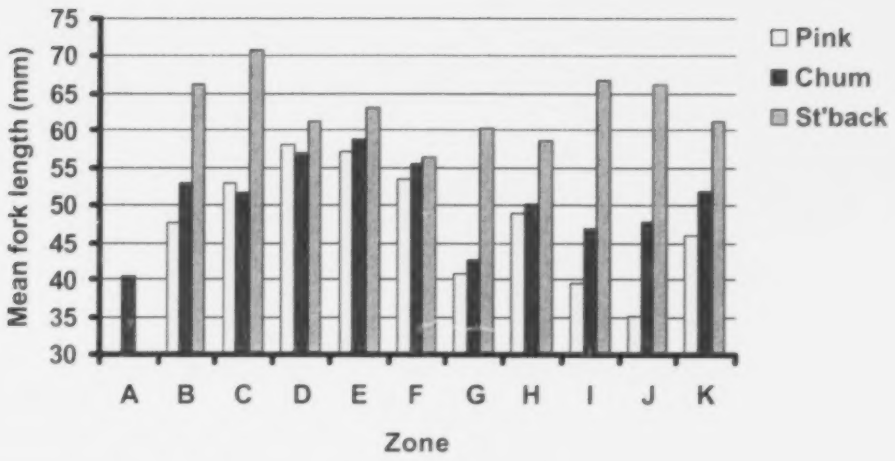

Figure 6. Mean fork length of juvenile pink and chum salmon and of 3-spine sticklebacks among zones.

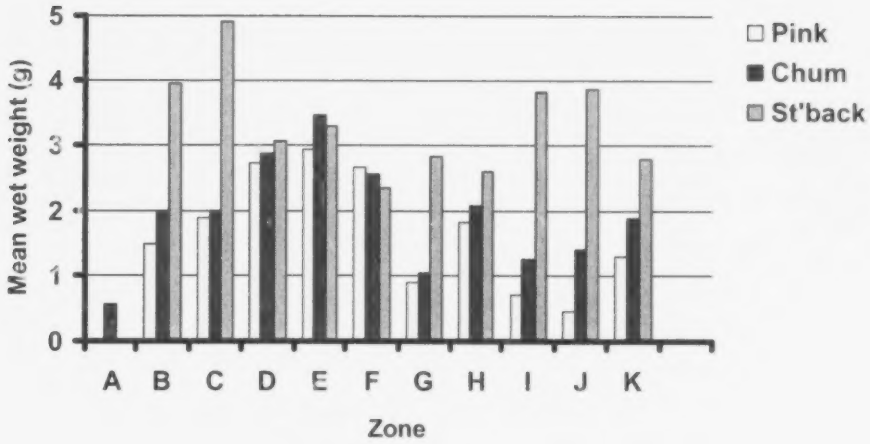

Figure 7. Mean wet masses of juvenile pink and chum salmon and of 3-spine sticklebacks among zones

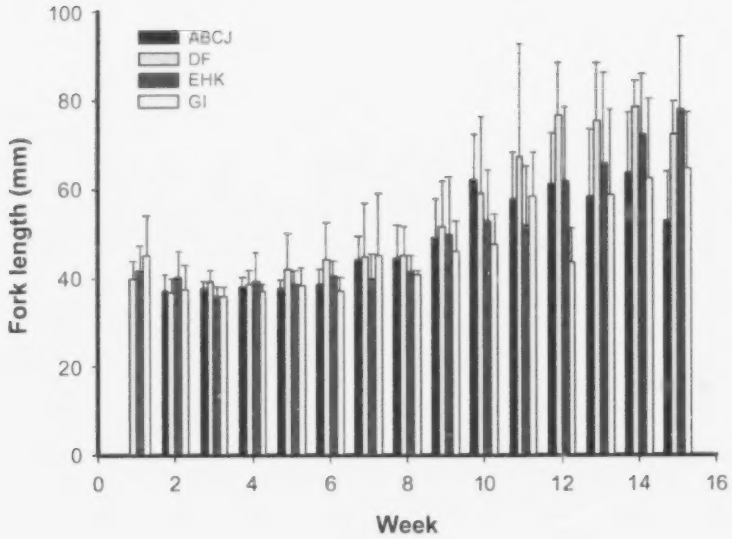

Figure 8. Mean fork length of chum salmon from consolidated areas throughout the study. Error bars are 1 standard deviation.

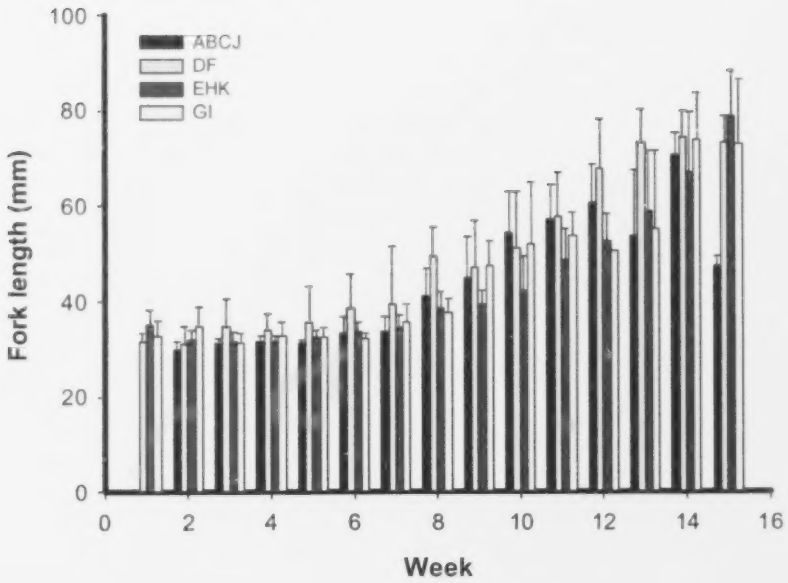

Figure 9. Mean fork length of pink salmon from consolidated areas throughout the study. Error bars are 1 standard deviation.

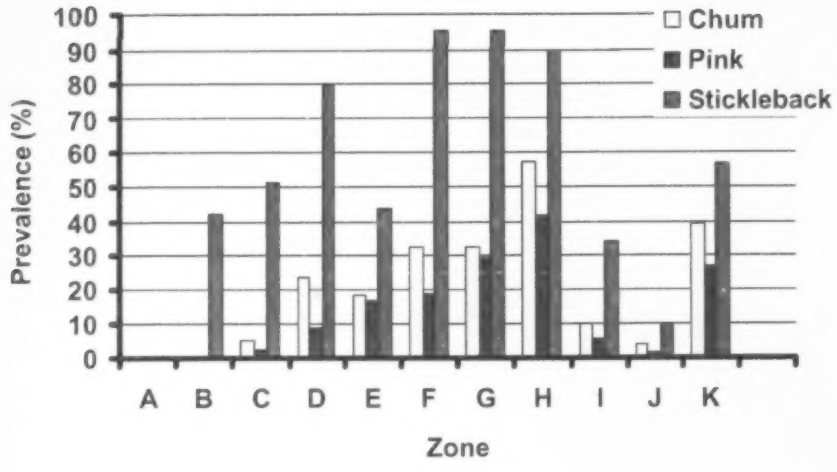

Figure 10. Prevalence of all non-motile stages on juvenile pink and chum salmon and on 3-spine sticklebacks by zone.

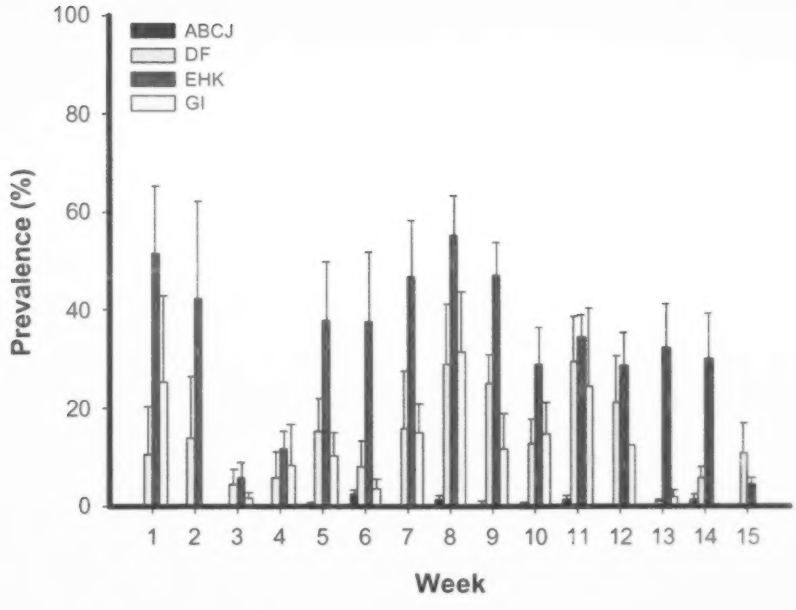

Figure 11. Prevalence of all non-motile (immature) sea lice stages on pink salmon from consolidated areas throughout the study. Error bars are standard error of the mean.

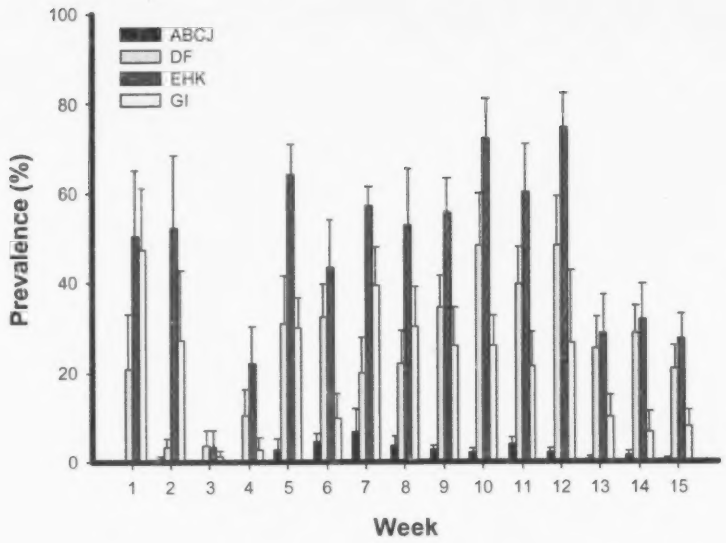

Figure 12. Prevalence of all non-motile (immature) sea lice stages on chum salmon from consolidated areas throughout the study. Error bars are standard error of the mean.

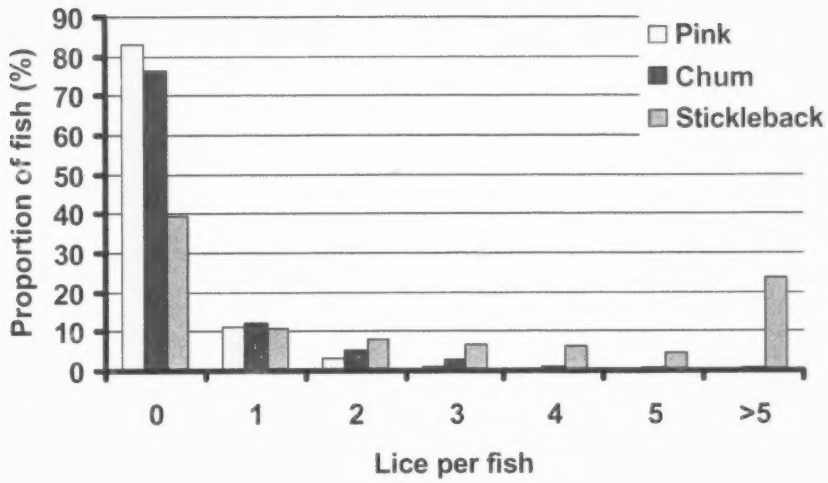

Figure 13. Distribution of all non-motile stages among juvenile pink and chum salmon and 3-spine sticklebacks

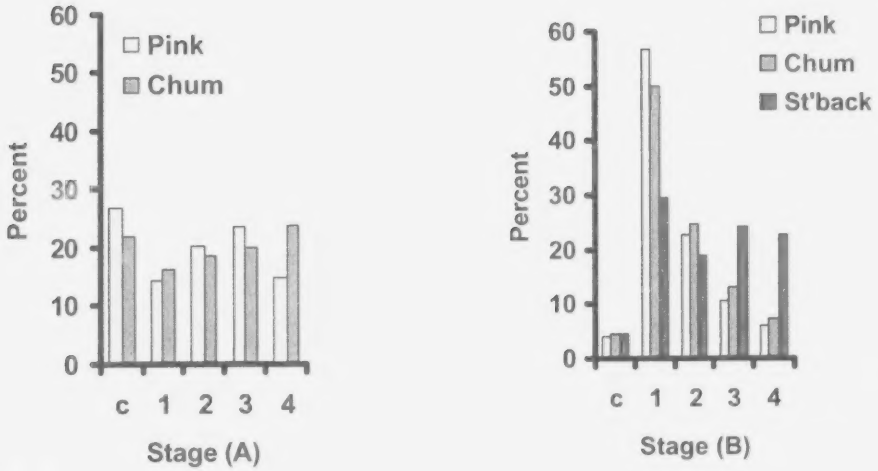

Figure 14. Distribution of copepodid and chalimus stages of *Lepeophtheirus* (A) and *Caligus* (B) on juvenile pink and chum salmon and on 3-spine sticklebacks. C, copepodid; 1, chalimus 1; 2, chalimus 2; 3, chalimus 3; 4, chalimus 4

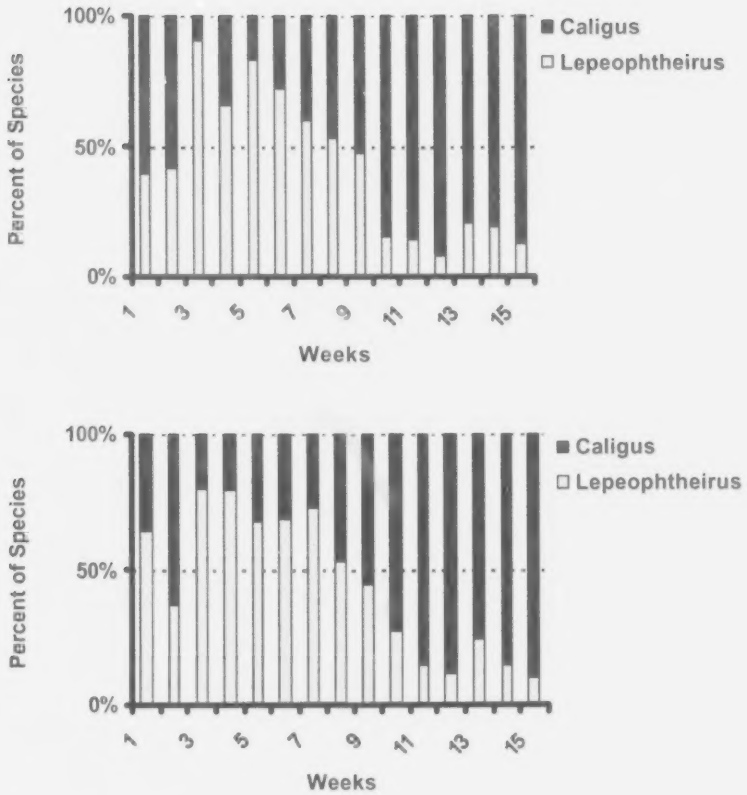

Figure 15. Relative proportion of copepodid and chalimus stages of *Caligus* and *Lepeophtheirus* on juvenile pink (top) and chum salmon (bottom) by week. Weekly samples sizes of chalimus are (from pink): 66, 29, 32, 98, 64, 18, 134, 114, 133, 92, 150, 94, 58, 79 and 23. Sample sizes (from chum): 100, 49, 20, 128, 277, 115, 193, 97, 330, 254, 513, 423, 180, 203 and 206.

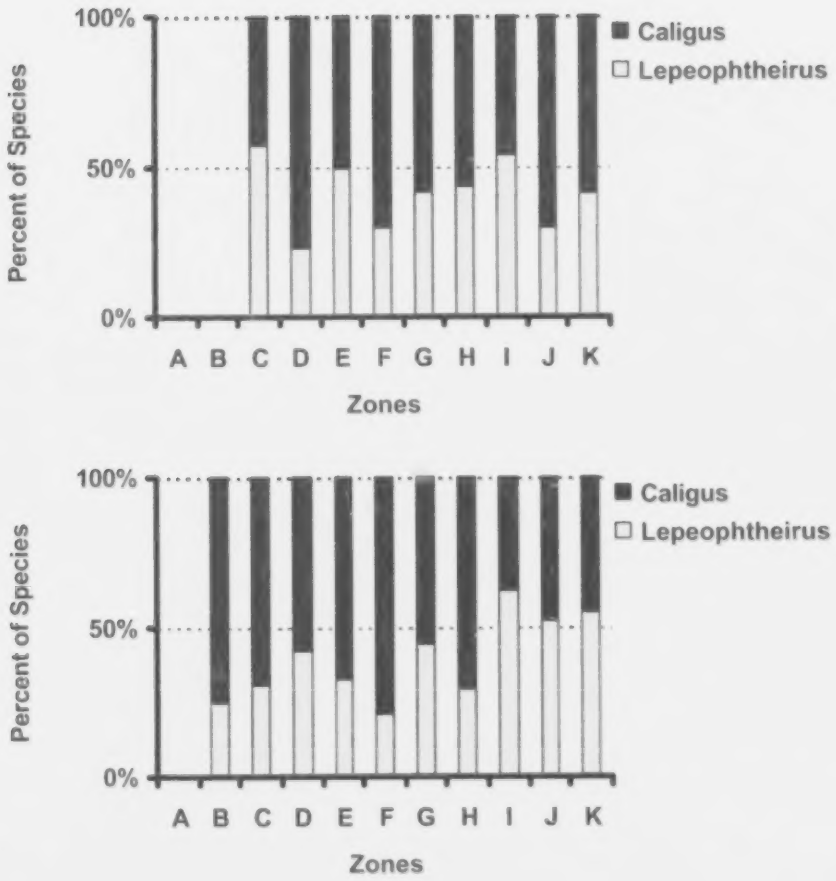

Figure 16. Relative proportion of chalimus stages of *Caligus* and *Lepeophtheirus* on juvenile pink (top) and chum salmon (bottom) by zone. Samples sizes of chalimus in each zone are (from pink): 7, 75, 65, 147, 99, 376, 26, 10 and 379. Sample sizes (from chum): 4, 33, 250, 217, 637, 349, 1056, 88, 46 and 408.

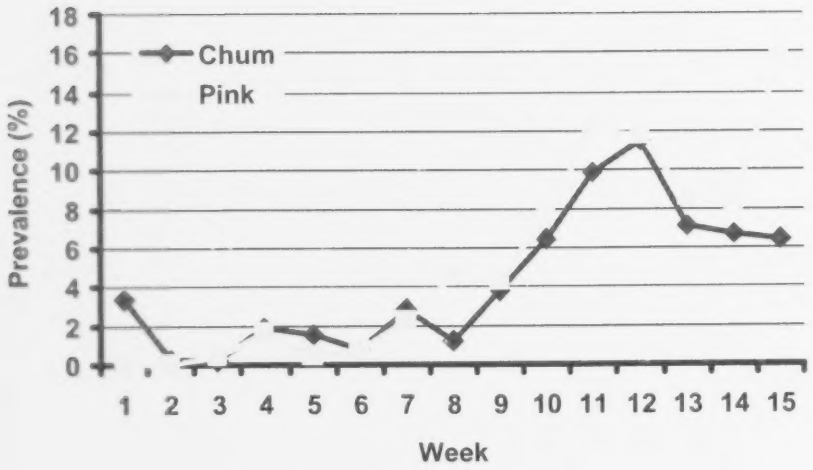

Figure 17. Weekly prevalence of motile *Lepeophtheirus salmonis* on juvenile pink and chum salmon

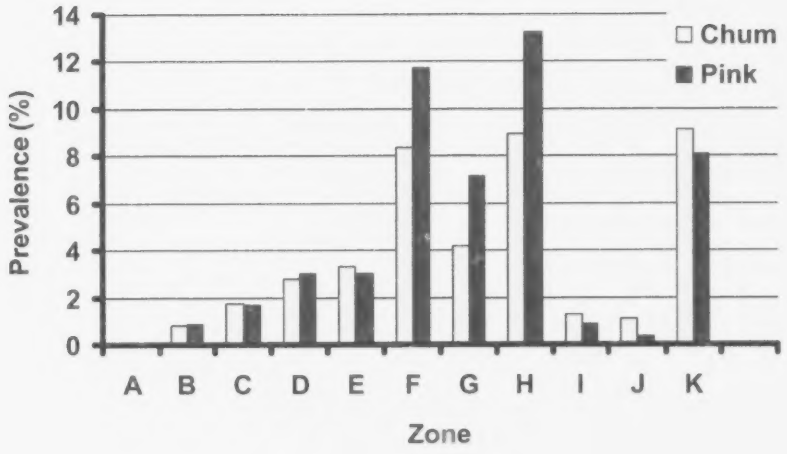

Figure 18. Prevalence of motile *Lepeophtheirus salmonis* on juvenile pink and chum salmon among zones.

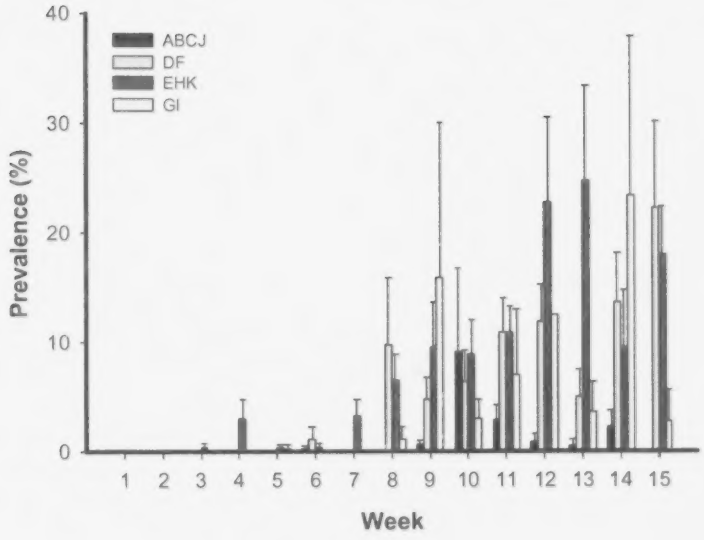

Figure 19. Mean prevalence of motile *Lepeophtheirus salmonis* on pink salmon by consolidated areas throughout the study. Error bars are standard error of the mean.

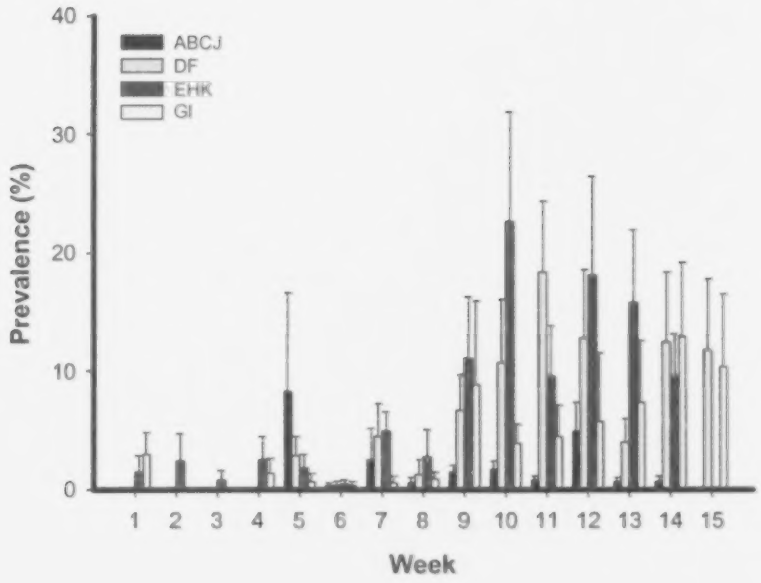

Figure 20. Mean prevalence of motile *Lepeophtheirus salmonis* on chum salmon by consolidated areas throughout the study. Error bars are standard error of the mean.

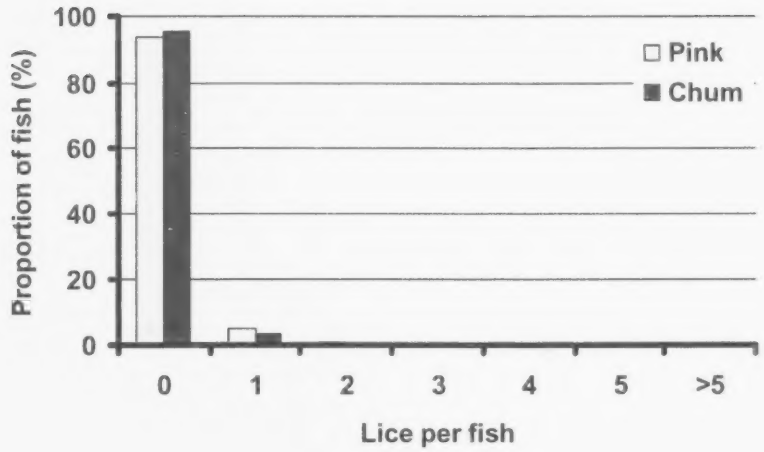

Figure 21. Distribution of motile *Lepeophtheirus salmonis* among juvenile pink and chum salmon

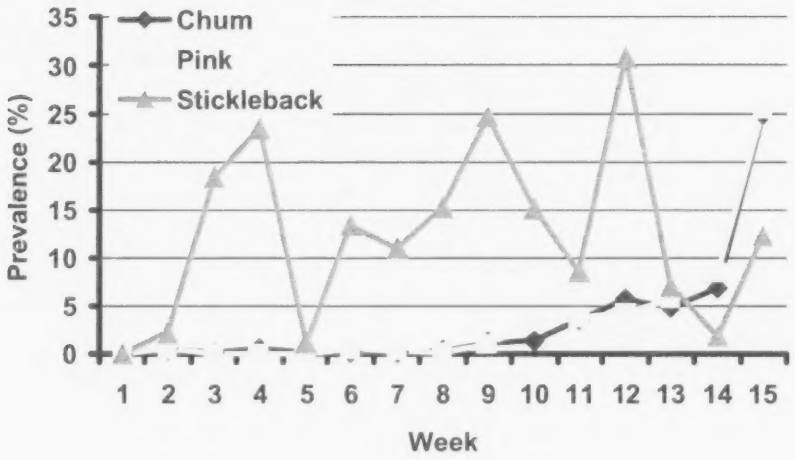

Figure 22. Weekly prevalence of motile *Caligus clemensi* on juvenile pink and chum salmon and on 3-spine sticklebacks

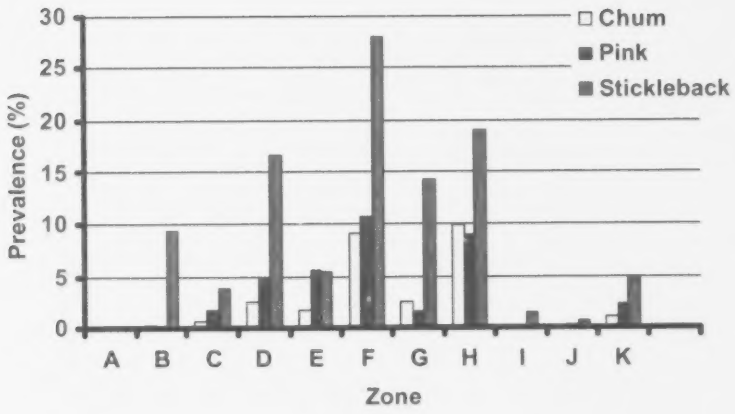

Figure 23. Prevalence of motile *Caligus clemensi* on juvenile pink and chum salmon and on 3-spine sticklebacks among zones

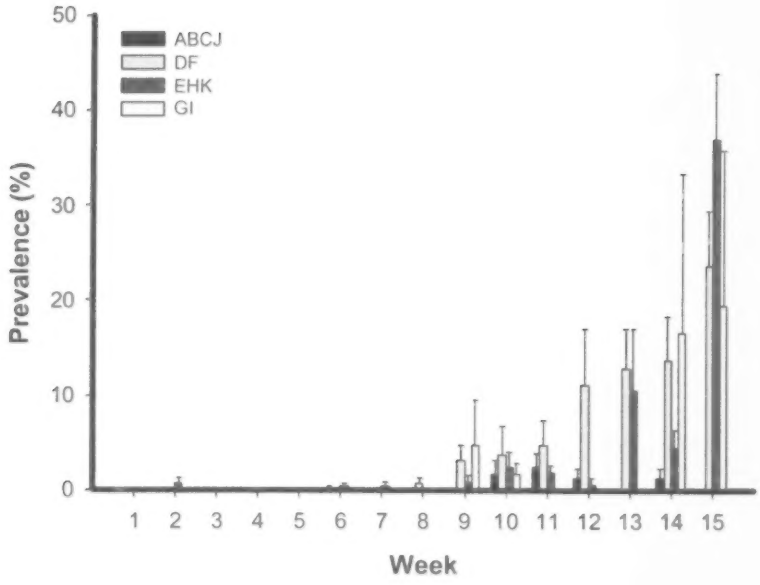

Figure 24. Mean prevalence of motile *Caligus clemensi* on pink salmon by consolidated areas throughout the study. Error bars are standard error of the mean.

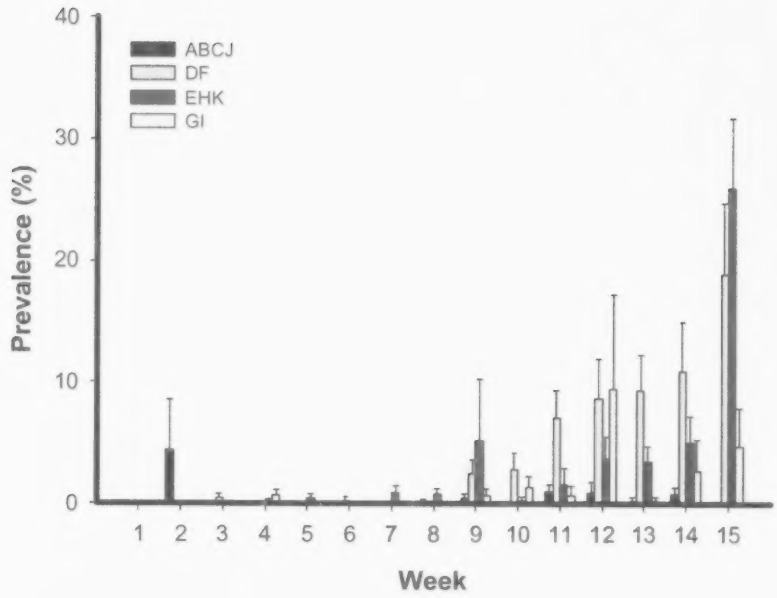

Figure 25. Mean prevalence of motile *Caligus clemensi* on chum salmon by consolidated areas throughout the study. Error bars are standard error of the mean.

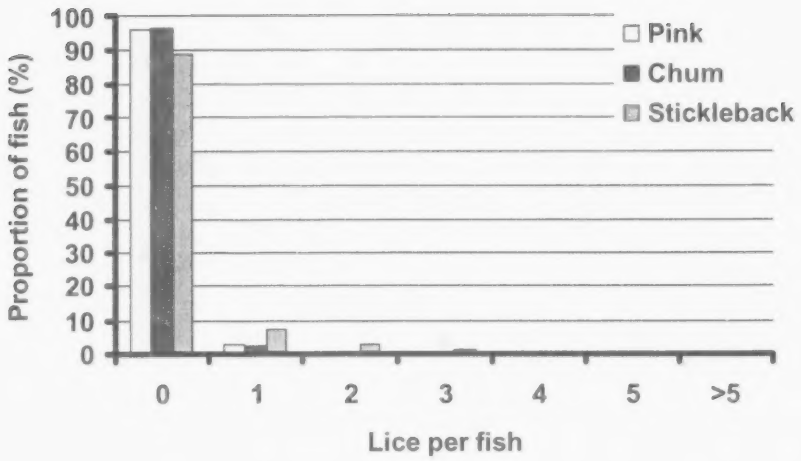

Figure 26. Distribution of motile *Caligus clemensi* among juvenile pink and chum salmon and 3-spine sticklebacks

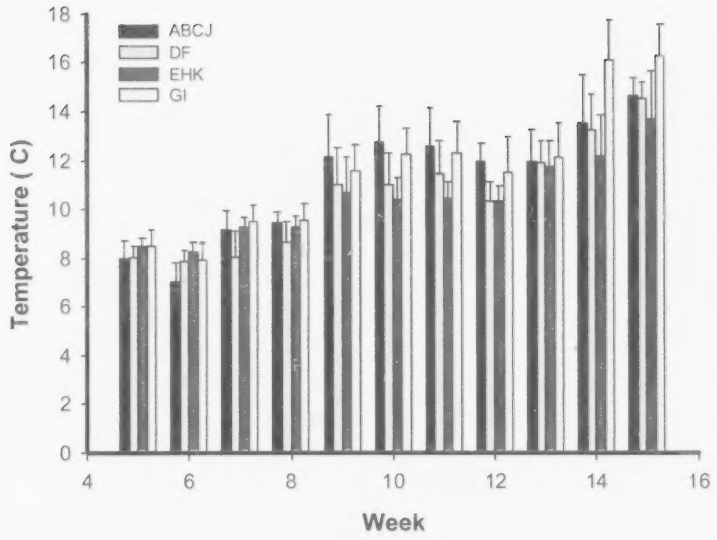

Figure 27. Mean weekly surface seawater temperatures in consolidated areas during weeks 5 to 15. Error bars are 1 standard deviation.

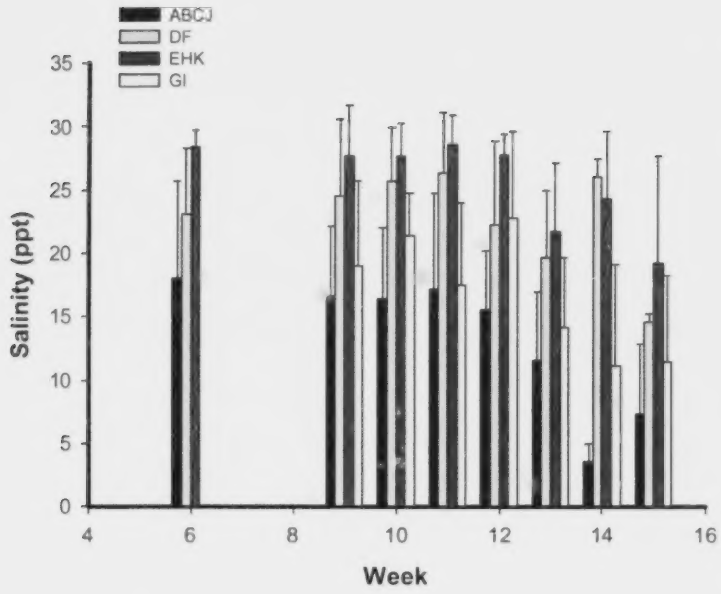

Figure 28. Mean surface seawater salinity among consolidated areas in weeks six and between weeks 9 and 15. Error bars are 1 standard deviation

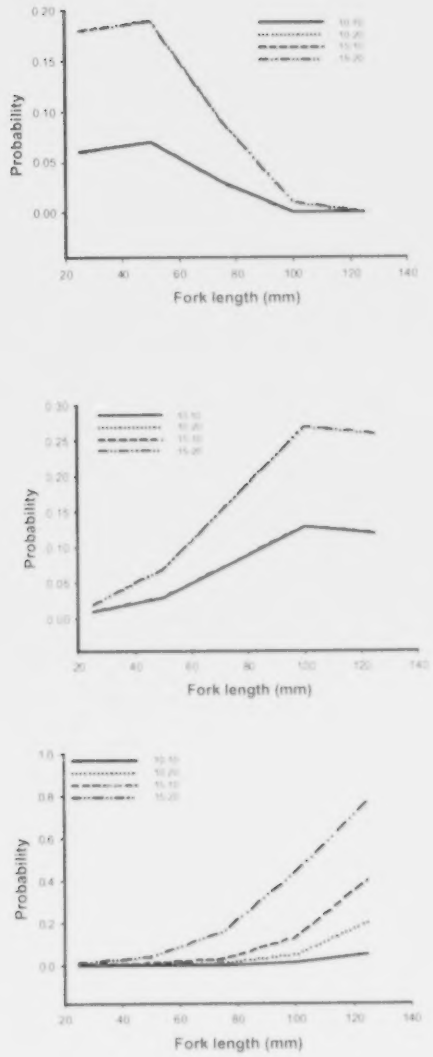

Figure 29. Estimated probabilities that juvenile pink salmon collected from area EHK are infected with sea lice for various fork lengths, temperatures and salinities (logistic regression model definition and coefficients are given in the text and Table 17, respectively). (top) immature stages of *Lepeophtheirus salmonis* and *Caligus clemensi*; (middle) motile stages of *L. salmonis*; (lower) motile stages of *C. clemensi*. 10-10, 10°C and 10ppt; 10-20, 10°C and 20ppt; 15-10, 15°C and 10ppt; 15-20, 15°C and 20ppt.

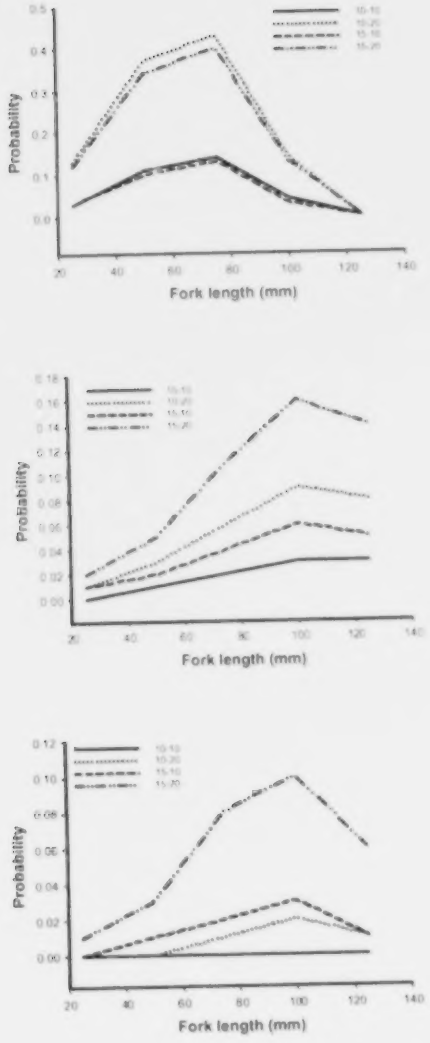

Figure 30. Estimated probabilities that juvenile chum salmon collected from area EHK are infected with sea lice for various fork lengths, temperatures and salinities (logistic regression model definition and coefficients are given in the text and Table 17, respectively). (top) immature stages of *Lepeophtheirus salmonis* and *Caligus clemensi*; (middle) motile stages of *L. salmonis*; (lower) motile stages of *C. clemensi*. 10-10, 10°C and 10ppt; 10-20, 10°C and 20ppt; 15-10, 15°C and 10ppt; 15-20, 15°C and 20ppt.

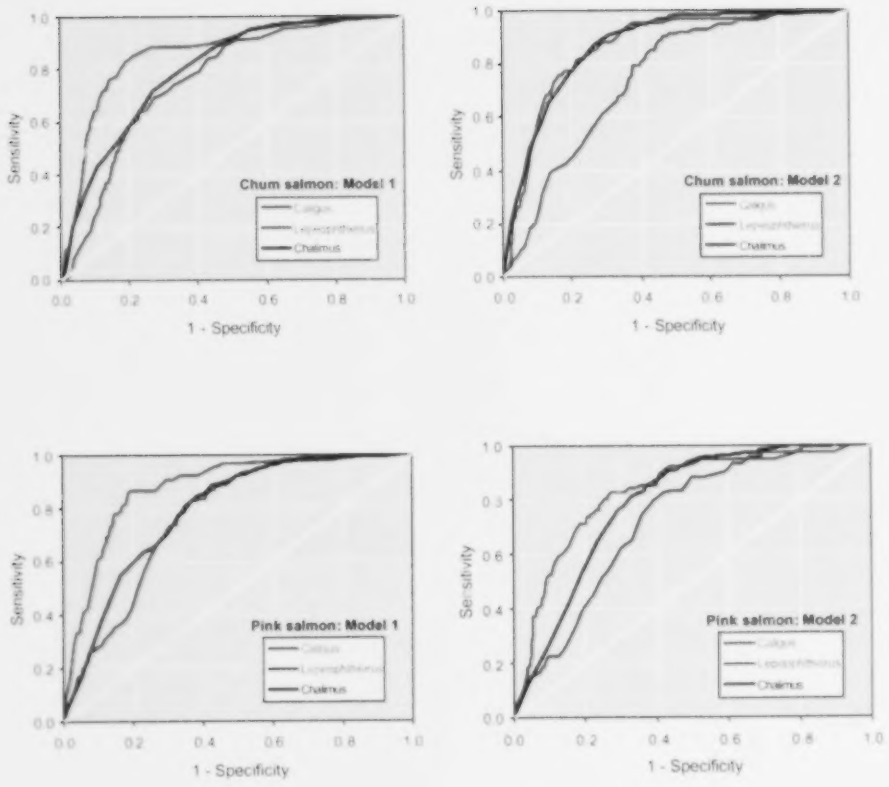

Figure 31. Receiver Operating Characteristic (ROC) curves displaying the relative predictive power of logistic regression models 1 and 2 for each host-parasite data set.

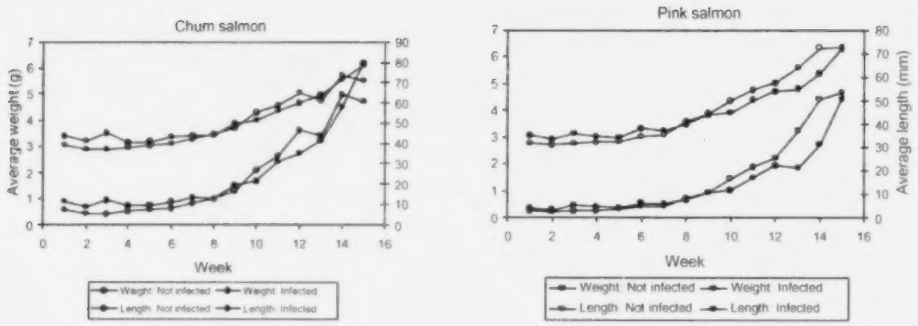

Figure 32. Size of uninfected juvenile chum and pink salmon and those infected with non-motile stages of *Lepeophtheirus* and *Caligus*

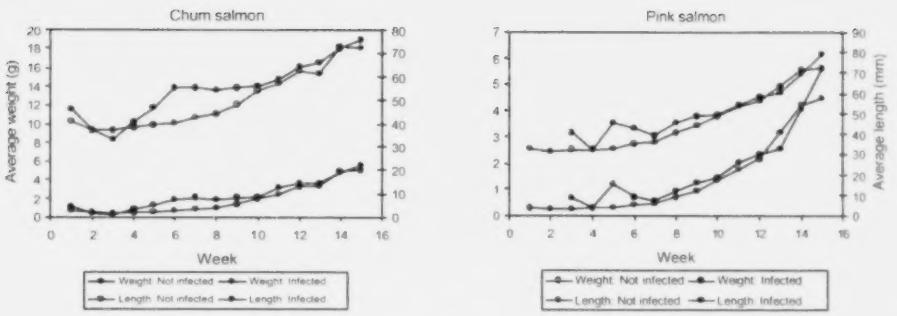

Figure 33. Size of uninfected juvenile chum and pink salmon and those infected with motile *Lepeophtheirus salmonis*

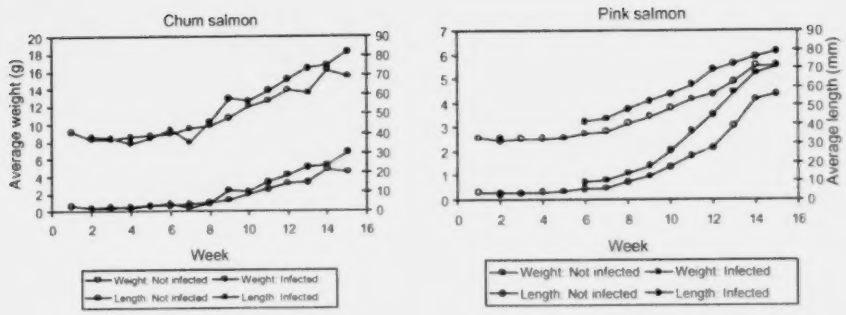

Figure 34. Size of uninfected juvenile chum and pink salmon and those infected with motile *Caligus clemensi*

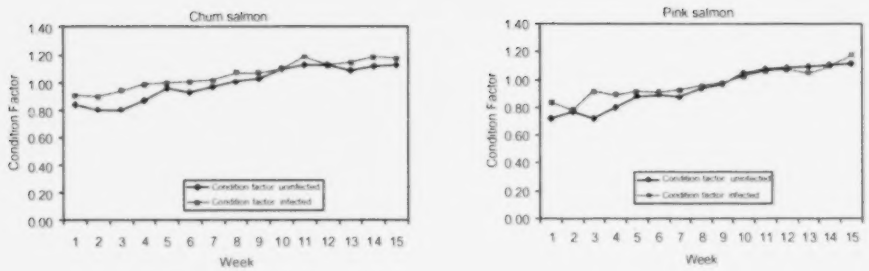

Figure 35. Fulton's condition factor (k=100 x weight / length^3) in uninfected juvenile chum (left) and pink (right) salmon and those infected with non motile stages

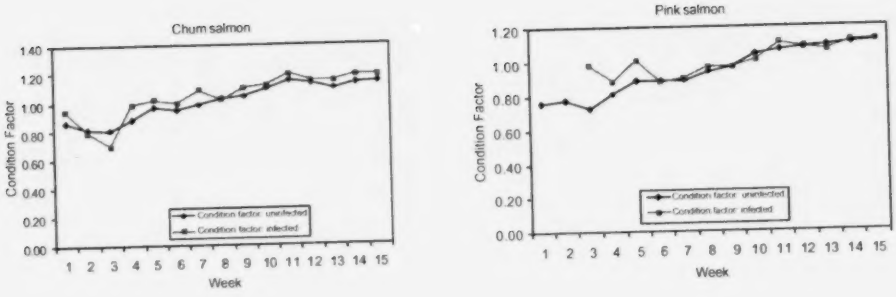

Figure 36. Fulton's condition factor (k=100 x weight / length^3) in uninfected juvenile chum (left) and pink (right) salmon and those infected with motile *Lepeophtheirus salmonis*

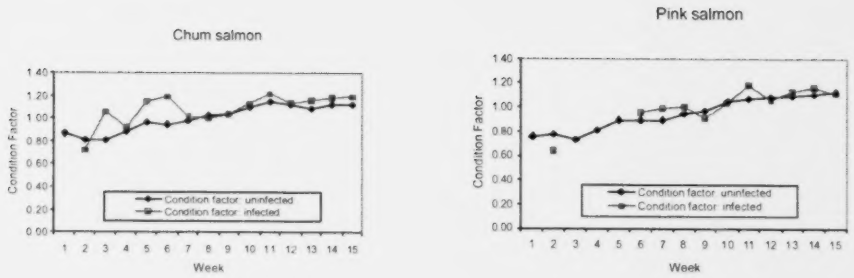

Figure 37. Fulton's condition factor (k=100 x weight / length^3) in uninfected juvenile chum (left) and pink (right) salmon and those infected with motile *Caligus clemensi*

Appendix 1. Criteria used to identify sea lice to species and stage.

species / Stage		*Caligus clemensi*	*Lepeophtheirus salmonis*
Copepodid	Free	• Frontal filament absent • Maxilliped slightly flattened, long, narrow, medial margin armed with three spiniform processes, basal segment two spiniform processes	• Frontal filament absent • Maxilliped shorter than *Caligus*, shaft, claw with one branching barb near base of latter
	Attached	• Frontal sac, filament present • Maxilliped slightly flattened, long, narrow, medial margin armed with three spiniform processes, basal segment two spiniform processes	• Frontal sac, filament present • Maxilliped shorter than *Caligus*, shaft, claw with one branching barb near base of latter
Chalimus	I	• First antenna armed with three unarmed setae • First leg only one seta on endopod • Fourth leg absent • Cephalothorax very sharp triangle type	• First antenna armed with seven unarmed setae • First leg two setae on endopod • Fourth leg present
	II	• 2 to 3 times larger than CH. I • Legs less distinct than CH.I • Thoracic segment present: five • Body ratio 2:1 • Cephalothorax triangular	• 2 to 3 times larger than CH. I • Thoracic segment absent • Cephalothorax and body segments indistinct
	III	• Frontal plates poorly discernible than CH. IV • Second leg not plate-like • Third leg distinct	• Second leg plate-like • Third leg very reduced • Genital segment absent protrusion

species / Stage		*Caligus clemensi*	*Lepeophtheirus salmonis*
		• Body ratio 3:1	
	IV-F	• Frontal plates well discernible • Genital segment broad , rectangular, and triangle basal form	• Filament attachment present • Genital segment two protrusions
	IV-M	• Frontal plates well discernible • Genital segment narrow and rounded shape	• Filament attachment present • Genital segment round without protrusions
Preadult	F	• Lunules distinct • Frontal plates fully developed • Frontal filament present • Genital segment rectangular • Genital segment poorly developed	• Frontal plates fully developed • Genital segment less developed and abdomen indistinct (Preadult I) • Genital segment fully developed and abdomen distinct (Preadult II)
	M	• Lunules distinct • Frontal plates fully developed • Frontal filament present • Genital segment long and round • Genital segment poorly developed	• Frontal plates fully developed • Gonads indistinct (Preadult I) • Gonads distinctly developed (Preadult II)
Adult	F	• Lunules distinct • Frontal plates fully developed • Maxilliped with two spinules on corpus inner margin • Genital segment length equal to thoracic zone • Gonads fully developed	• Genital segment subquadrangular, longer than thoracic zone of shield, with rounded posterior lobes • Lunules absent • Purple coloring
	M	• Lunules distinct • Frontal plates fully	• Genital segment oval, about as long as

species / Stage		*Caligus clemensi*	*Lepeophtheirus salmonis*
		developed • Maxilliped with denticulated flange on corpus inner margin • Genital segment less than ½ length of thoracic zone • Gonads fully developed	thoracic zone of dorsal shield • Lunules absent • Purple coloring

Appendix 2. Illustration of a Receiver Operating Characteristic (ROC) curve